Chapter IX

Fish and Amphibians at Emerald Lake

Introduction

Background

Many lakes and streams in the High Sierra are sensitive to acidic deposition, and acid precipitation is known to occur in these mountains. The lakes and streams in the Emerald Lake watershed are representative of subalpine and alpine Sierran waters, and potential changes in the chemistry and biology of these waters provide excellent early-warning signals of acid deposition impacts. Changes in vertebrate populations, particularly fish and amphibians, have accompanied cultural acidification in the northeastern United States, Canada, and Scandinavia. These population effects include reproductive failure, alterations in size and age structures, changes in growth rates, disruption of social behavior, and extinction. Fish and amphibian populations, then, are sensitive indicators of environmental stress owing to acidic inputs. The research described below is part of the Integrated Watershed Study (IWS) supported by the California Air Resources Board. This research has provided baseline data on the population and behavioral characteristics of fish and amphibians in the Emerald Lake basin. Data collected from the fish and amphibian study will be used in concert with data from other IWS projects to assess the current status of, and stresses to, High Sierra waters.

Our study sites include lakes, streams, and ponds in the watershed of the Marble Fork of the Kaweah River, including Emerald, Aster, Heather, and Pear Lakes, associated inlet and outlet streams, and ponds in the vicinity of Emerald Lake (Fig. IX-1). We have found only two common aquatic vertebrate species in this study area: the brook trout or brook char (Salvelinus fontinalis) and the Pacific tree frog (Hyla regilla). Brook trout are the only fish present in the study lakes and associated outlet streams. Brook trout were stocked in the study lakes from the 1920s to the 1960s, but current populations are maintained by natural reproduction. This species is one of the most widely distributed fish in high elevation Sierra Nevada lakes and is of considerable recreational importance. In the Emerald Lake basin larvae of Pacific tree frogs are found primarily in ponds.

The brook trout and its relatives in the genus Salvelinus are among the species most affected by acidification in the European and Atlantic seaboard areas, so their physiological tolerances have been extensively investigated. Brook trout can be harmed by direct effects of low pH and elevated aluminum concentrations, or through indirect effects on habitat and trophic structure. All individuals are killed within hours at pH 4.1 or less, and young fish are less able to tolerate temporary exposure to low pH than adults (Robinson et al. 1976). When exposure to acid conditions is frequent or chronic the tolerance of brook trout is far less, and they are usually not found in natural habitats with pH lower than 4.2 - 5.0 (Lennon 1967, Magnuson et al. 1984, Schofield 1976). At pH 5.16 growth of reproductive adults is reduced considerably, which reduces their egg production. Although gametogenesis proceeds normally down to pH 4.48, ovulation, and thus spawning time, is delayed significantly at 5.56 (Tam and Payson 1986). In one study the mobility of spermatozoa declined below pH 5.0, water absorption of newly-laid eggs declined below pH 5.2 or 4.5 (depending on the source of the parent stock), and egg survival decreased below pH 4.0 (St. Pierre and Moreau 1986). In another study all developmental stages of brook trout were continuously exposed to pHs of 4.5, 5.0, 5.5, 6.0, 6.5, and 7.1 (Menendez 1976). The production of viable zygotes by natural spawning was lower at pH 5.0 than pH 6.5 and hatching success declined at pH 6.5 and was negligible below 5.0. Growth and survival of sac fry from hatching through emergence from the natal gravel were reduced at pH 6.5, and mortality approached 100% at 5.0 if the parents were continuously exposed to these pH levels (Menendez 1976). Substantial mortality of adult fish only occurred when pH was reduced to 4.4. Trojnar (1977) also reported reduced egg hatchability with decreased pH, although mortality was not as great as in Menendez (1976). Survival of sac fry depended on the pH at which pre-hatching embryos were incubated, suggesting some acclimation of early trout stages to decreased pH (Trojnar 1977). These and other studies indicate that fish recruitment failure in acidic conditions is primarily related to increased mortality of early egg and fry stages (Leivestad et al. 1976, Peterson et al. 1982), although adult mortality occasionally occurs (Leivestad and Muniz 1976).

The effects of low pH on fish are also influenced by the concentration of other ions (Brown 1980, Fromm 1980, Trojnar 1977). In particular, moderate to high concentrations of calcium mitigate deleterious effects of increased acidity (Brown 1982). The effects of low pH on fish physiology are dependent on calcium levels. At low pHs and high calcium levels increased mucus production on gill surfaces and a disruption of the acid-base balance in blood can result in severe respiratory stress. On the other hand, at moderately low pHs and low calcium concentrations ionoregulation failure, typified by large losses of chloride and sodium, can result in mortality (Leivestad 1982). Because soft, slightly acidic, unbuffered waters are most susceptible to acidification, loss of fish in these waters is probably related to disruption of ionoregulation which may ultimately result in circulatory collapse (Wood and McDonald 1982). Increased mobilization of metals, in particular aluminum, at low pHs may also have a variety of effects on fish. At concentrations recorded for some acidified waters, aluminum is directly toxic to brook trout (Schofield and Trojnar 1980). Aluminum toxicity is dependent on pH, being greatest at ca. pH 5.0 (Schofield and Trojnar 1980). At pHs 4.2 to 5.6 survival and growth of brook trout sac fry are lower when aluminum is present; however, at pHs 4.2 to 4.8 the survival of brook trout eggs is enhanced by the presence of aluminum (Baker and Schofield 1982). High aluminum concentrations often result in mucus clogging of the gills and changes in blood acid-base balance (McCahon et al. 1987, Leivestad 1982). Free aluminum ions appear to be extremely toxic to fish, and organic chelators may ameliorate the effects of high aluminum concentrations by binding aluminum ions (Baker and Schofield 1980). This is probably why many fish can tolerate greater acidity in bog waters than in waters acidified by inorganic acids. Finally, aluminum toxicity is modified by calcium levels (Carroll et al. 1979). Effects of acidification on aquatic systems, then, will depend on the chemistry of receiving waters and will often reflect the complex interaction of hydrogen, aluminum, and calcium ions.

Various strains of brook trout show different susceptibilities to acid stress (Swarts et al. 1978, Robinson et al. 1976). In addition, some life history stages of trout may acclimate to low pHs, although the evidence is hardly conclusive (Trojnar 1977, Swarts et al. 1978). Behavioral responses of fish to low pH may include decreased activity levels, decreased feeding and decreased reaction to chemical stimuli, as well as increased thigmotaxis (attraction to surfaces) (Jones et al. 1987).

These direct responses of trout to increased acidification are reflected in changes in their population structure. Many population parameters of fish, including recruitment, survival, size or age structure, and growth, change in response to changes in pH (Fish and Wildlife Service 1982a and 1982b, Johnson 1982, D'Itri 1982, NRC Canada 1981, Frenette and Dodson 1984, Harvey 1982). The reduced abundance or disappearance of brook trout from acid-stressed systems is usually related to recruitment failure (Haines 1981, Spry et al. 1981), although mortalities of juveniles and adults have been reported in some studies (Schofield 1977). In an 8-year lake acidification experiment, Schindler et al. (1985) found complete reproductive failure in lake trout (Salvelinus namaycush) at pH 5.4. At pH 5.1 the condition of adult trout declined drastically with the collapse of their food supply. Because of recruitment failure, the size structure of fish populations often changes to one dominated by larger, older fish (Ryan and Harvey 1980, 1981, Schofield 1976). In some instances, however, older fish may be absent from systems exposed to increased acidity because of increased mortality following spawning (Frenette and Dodson 1984, Rosseland et al. 1980). Most laboratory studies indicate that fish grow more slowly at lower pHs (Muniz and Leivestad 1979, Rodgers 1984). In the field, however, some fish populations will actually grow at higher rates following acidification because lowered fish densities reduce competition (Almer et al. 1974, Jensen and Snekvik 1972). Field growth rates, then, will represent the results of antagonistic responses to metabolic stress and decreased competition. Fish in acidic waters often have higher condition factors than those in nonacidic waters owing to a release from competition (Harvey 1982).

Increased acidification may also affect fish indirectly by altering the abundance and species composition of prey assemblages, and by altering habitat characteristics (USFWS 1982). In the latter case, increased growth of filamentous algae, fungi, and mosses following acidification may make gravel beds unsuitable for spawning. Brook trout often avoid areas of high acidity in lakes and streams, so their responses to acidification may depend on the presence, accessibility, and extent of less acidic refuge areas (Hall et al. 1980, Johnson and Webster 1977).

Effects of low pH on amphibians have been less studied, but their larval habitats are often small, poorly-buffered, and naturally acidic. Furthermore, vulnerable early life stages are present in the spring when ponds are filled by spring rains or snow melt. The available evidence suggests that fish and amphibian populations respond similarly to acidification (NRC Canada 1981). Many species of amphibians do not show increased mortality until pH is reduced below 4.0 (Pierce 1985), although difficulties in egg hatching and metamorphosis for some species begin as the pH drops below 5.0 (Clark and LaZerte 1985). There is also considerable intraspecific variation in acid tolerance of early life stages of amphibians, both between and within populations (Cook 1983, Pierce 1985, Pierce and Sikand 1985, Pierce et al. 1987, Pierce and Harvey 1987). Sublethal effects of increased acidity include reduced larval growth and an increase in the incidence of physical abnormalities (Pierce 1985, Tome and Pough 1982, Pierce and Harvey 1987). Fertilization of gametes is the event most sensitive to acid inputs; pre-hatching embryonic stages are usually more sensitive to increased acidity than larvae, and acid tolerance increases as larvae grow (Pierce 1985). In turn, larvae appear to have lower acid tolerances than adults (Mathews and Larson 1980). Amphibian populations have been reduced or lost as a result of increased acidification (Pough 1976, Cooke and Frazen 1976, Hagstrom 1977, Strijbosch 1979), and the number of species of amphibians tends to decline with increased acidity (Pierce 1985).

Reduced hatching of amphibian eggs at low pH is apparently related to decreased fluid uptake across membrane surfaces and to inhibition of the activity of hatching enzymes. As in fish, the physiological mechanisms accounting for acidification effects on amphibian larvae are related to ionoregulation. Hydrogen ions interfere with sodium exchange across membranes, and high calcium levels mitigate many of the effects of high hydrogen ion concentration (Pierce 1985).

It is evident from the above that fish and amphibian populations provide many well-studied indices for assessing the effects of cultural acidification on freshwater systems. The effect of acid inputs on particular lake and stream systems would depend on their chemical and biological characteristics and the genetic composition of their vertebrate populations. However, we can predict that increased acidification will reduce population sizes, change age or size structure and individual growth rates, increase mortality of early life stages, delay maturity and egg hatching, decrease fecundity and fertility, delay or inhibit spawning, and modify reproductive and feeding behaviors. In the fish/amphibian investigations, we have described these population characteristics of brook trout and Pacific tree frogs to assess the current condition of, and predict effects of increased acidification on, fish and amphibians in the High Sierra.

Objectives

The overall objective of this research was to evaluate the current status of aquatic vertebrate populations in the Emerald Lake watershed and nearby systems. We achieved this objective by examining the population characteristics of fish and amphibians in these aquatic systems. We (1) censused fish populations and estimated fish growth rates in Emerald Lake and its outflow stream, (2) studied the reproductive biology of fish in the Emerald Lake system, including egg production, hatching success, and recruitment of young, (3) determined survivorship for early life history stages of fish in this system, (4) investigated seasonal changes in fish behavior, including diet and movement patterns, (5) compared the population sizes, growth rates, and size and age structures of Emerald Lake Basin fish to those in other lakes and streams in the Marble Fork Drainage, and (6) characterized larval amphibian habitats in the Emerald Lake basin. By examining year-to-year variation in our data, and by comparing these data with literature values and data collected by other IWS projects, we have determined the current status of, and stresses to, aquatic vertebrate populations in the Emerald Lake basin, and can predict the probable responses of these populations to possible increased acidic inputs.

History of project

The fish/amphibian project was an extension of on-going limnological investigations conducted at Emerald Lake with support from the California Air Resources Board (CARB). Building on research supported by funds from the Co-operative Park Service Unit, CARB-funded limnological investigations at Emerald Lake began in the summer of 1984. The Emerald Lake watershed was chosen by the California Air Resources Board as the site for its Integrated Watershed Study because it is sensitive to acid deposition, representative of subalpine and alpine waters in the Sierra Nevada, and accessible at all times of the year. The overall purpose of the Integrated Watershed Study is to assess the current status of a representative Sierran system and to determine current and potential responses to acidic inputs. The CARB limnological investigations at Emerald Lake included monitoring water chemistry and the populations of planktonic and benthic organisms, as well as experimentation to predict the effects of increased acidification on stream and lake organisms (Melack et al. 1987; Cooper et al. 1988b).

Fish populations were studied as part of the limnology project (Melack et al. 1987) in the summer of 1984. At the beginning and end of the summer fish populations in the Emerald Lake outflow stream were censused, size structure was determined, and some fish were sacrificed for age and diet analyses. In addition, lake fish were observed while snorkeling, and a few lake fish were sacrificed for age and diet analyses at the beginning of the summer. On the basis of these investigations and literature reports, the CARB called for a detailed study of aquatic vertebrate populations in the Emerald Lake area. The justifications for this project included: (1) population characteristics of fish and amphibians are sensitive indicators of acid stress; (2) fish are an economically important recreational resource in the High Sierra; (3) the study of fish and amphibian populations requires special techniques and intensive research effort, and thus could not be accommodated within existing projects. Amphibian studies were also included because larval amphibian habitats are small and poorly-buffered, and therefore vulnerable to acidic inputs.

The first phase of the fish/amphibian project was funded by CARB from July 1985 to July 1987. In those two years we measured the population sizes, survival, reproduction, growth, movements, size and age structure, and diets of brook trout in the Emerald Lake system and nearby lakes and streams in the Marble Fork of the Kaweah River drainage. The results were reported earlier (Cooper et al. 1988a). A third year of fish/amphibian work was funded by CARB as part of continued limnological investigations at Emerald Lake. Studies on fish and amphibians followed much the same course as earlier work, but we restricted our efforts to Emerald Lake and its outflow system and placed additional emphasis on the habits of brook trout during their first months of life. Because some aspects of the biology of our target organisms varied so greatly from year to year, we have combined, reanalyzed and reinterpreted the data from all three years. A summary of our findings is presented below.

Study Sites

Our study sites were four lakes and associated streams in the Marble Fork of the Kaweah River watershed (Fig. IX-1). The surface areas of Heather, Aster, Pear, and Emerald Lakes range from 1.8 to 7.6 ha, the maximum depths range from 6 to 26 m, and subsurface summer pHs range from 6.3 to 6.5 (Table IX-1). Detailed water chemistry data for these lakes are presented in Melack et al. 1987 and elsewhere in this report (Chapters II, II, and X). The brook trout, Salvelinus fontinalis, was the only fish species found in the four study lakes. The outlet streams of all four lakes had trout populations at the start of the study, but not all of these fish were long-term residents. In 1985 the outlets of Heather and Pear Lakes dried up completely, killing all of the resident trout. By summer of 1986 Heather outlet contained adult trout, but it once again dried up by autumn. The other streams retained some flow. In 1987, all of the study streams stopped flowing temporarily, but only the Heather and Pear outlets sustained total trout mortality. Since there were trout in all of the streams at the beginning of each summer, we assume that they were repopulated from their respective lakes following each decimation. Only Aster Lake contained trout in its inlet stream.

Most of our trout investigations focused on Emerald Lake and its outlet stream. After about 100 m the outlet of Emerald Lake enters a substantial pond, then a short cataract and a second pond of smaller size (Fig. IX-2). Our stream investigations concentrated on the 100-m outlet below Emerald Lake plus both downstream ponds. A third pond (Hidden Pond) located west of the Emerald Lake outlet enters the second pond through an intermittent rivulet. The stream then continues from the second pond to Aster Lake. All of these waters contain brook trout. The outlets of Heather, Aster and Pear Lakes consist largely of smooth, very shallow cataracts, waterfalls, and plunge pools. We studied a 100-m section of each of these outlet streams just below their respective lakes, a 100-m section of Aster's inlet stream just above Aster Lake, and a 100-m section between the ponds downstream from Emerald Lake and the Aster inlet.

In addition, we surveyed fifteen ponds in the Marble Fork watershed for the presence of amphibian larvae (Fig. IX-1). These ponds ranged from permanent bodies of water containing trout (e.g. Hidden Pond) to small ponds which dried up by mid- to late-summer. Larvae of the Pacific Treefrog, Hyla regilla, were found in twelve of these ponds, including Hidden Pond. In addition, Hyla larvae were sighted in Heather Lake, but were not found in any of the other lakes. The Mount Lyell Salamander (Hydromantes platycephalus) was sighted on two occasions in the Marble Fork basin.

Methods

Collection of Adults

Most fish were captured by angling in the study lakes, but in 1986 and 1987 several gill net sets were made to determine if angling selected fish of particular sizes or dietary preferences. The net employed was 43.5 m long, had a depth of 1.5 m, and was composed of equal-sized panels of 2.5 to 6.2 cm mesh in 0.6 cm gradations. In Emerald Lake in 1986, 17 fish were taken in a 4 hour set on 8 July, 15 were taken in a 4 hour set on 3 August, 13 were taken in a 3.5 hour set on 3 September and 14 were taken with a 4 hour set on 16 September. In Emerald Lake in 1987, 4 fish were taken with a set of one hour and 40 minutes on 11 July. Five to 10 fish from each of Heather, Aster, and Pear Lakes were also collected by gill net in early October 1986.

Adult fish in the first pond downstream from Emerald Lake (Pond 1) were captured with fyke nets in September 1986 and biweekly from mid-July to mid-September in 1987. The two fyke nets were composed of 7 hoops, each 0.9 m in diameter, with a bag 4.2 m long. One fyke net had two wings, each 7.5 m long, and the other had a single 6.8 m lead. Nets, wings, and leads were composed of 1.3 cm mesh. In all years fish in the second pond downstream from Emerald Lake (Pond 2) were seined during the period of low water in August-September. The seine was 5 m long and 1 m deep with 6 mm mesh. Small numbers of fish from both ponds were collected by angling for diet and fecundity analyses on 10 July 1986 and on 7 and 10 October 1987.

Adult fish in the streams were usually censused by three passes with an electrofisher and dip nets. However, Heather and Pear outlets became so small in late summer that we were able to capture all fish by intensive searching and hand netting. The Emerald and Heather Outlets were sampled in 1985, 1986, and 1987, but the other streams were only sampled in 1985. Fish moving between Emerald Lake, Emerald outlet and Pond 1 during spawning runs were captured in traps at both ends of the stream. In 1985 the pair of box traps at the lower end of the outlet were 46 X 30 X 30 cm deep with frames of 2 cm PVC covered by 6.4 mm plastic mesh; the lower trap captured upstream-migrating fish and the upper trap captured downstream-migrating fish. Fish migrating from the lake to the outlet were intercepted by a 1 meter long mesh cone leading to a 3.8 mm plastic mesh box. Fish migrating from the outlet to the lake were captured with a box trap similar in design to the two lower traps. In 1986 and 1987, traps at the lower end of the outlet had wooden frames with dimensions of 84 X 50 X 64 cm deep and were covered by 6.4 mm plastic mesh. The same traps used in 1985 were employed to capture fish migrating from the outlet to the lake. The trap used to capture fish migrating from the lake to the outlet was a 1 m long wood and 6.4 mm mesh trough with converging sides leading to a 3.8 mm mesh box. The traps used in the 1986 and 1987 spawning runs were also operated after snowmelt subsided in 1987, to determine the extent of movements outside of spawning season. The dates of operation were 7-16 July, 20 July-28 August and 9 September to the start of spawning season. The only movements recorded were from 8-11 July.

Collection of Underyearlings

Most young-of-year fish (YOY) collected for marking, measuring and diet analysis were taken by dip net during the day or by dip net with a light at night. Smaller numbers were captured by seine, fyke net, electrofishing, unbaited minnow trap, "slurp gun", drift net and the traps deployed seasonally at both ends of Emerald outlet.

Handling of Fish

After capture, adult fish were held in 6.4 mm mesh nylon bags placed in their original habitats. They were then transferred to a plastic bucket and anaesthetized with tricaine methanesulfonate for measurement, marking and sometimes stomach pumping. YOY were held in rigid mesh boxes before and after measuring and marking to evaluate handling mortality.

Size and age

Fish captured in lakes and streams were measured to the nearest millimeter and weighed to the nearest gram, 0.1 g or 0.01 gram depending on size. Most fish in the lakes were marked with Floy anchor tags (Rawstron 1973) modified with individually distinctive combinations of colored beads and released. Subsamples of fish were preserved for direct aging by counting otolith rings (Neilson and Geen 1981, Radtke and Dean 1982). Fish in the streams and fish in the lakes less than 12 cm long were individually marked by heat branding (Groves and Novotny 1965) in 1985 and by tattooing in 1986 and 1987 (Hart and Pitcher 1969; Pitcher and Kennedy 1977). Fish in the ponds were marked by Floy tags in 1985 and by tattooing in the other years. In conjunction with branding and tattooing, we also clipped adipose fins and small portions of the caudal fin to increase the number of combinations. Caudal fins quickly regenerated but new portions of the fin rays could be easily recognized.

Lipid Content

Samples of fish were frozen after capture and analyzed for whole body lipid by the method of Bligh and Dyer (1959) or Brett et.al. (1969). The latter method was used for most fish because it yielded dry weight (for % dry weight) and water content.

Population Size

Adult and juvenile lake fish were censused with mark-recapture techniques; i.e. marking and releasing fish caught by angling then comparing the numbers of marked and unmarked fish in subsequent snorkel surveys (Ricker 1958, 1975). In the surveys, we snorkeled a lake in a zig-zag pattern and counted the untagged and recently-tagged fish. The counts were then converted to population estimates with confidence limits (Ricker 1975). We used this technique in all lakes in 1985 but only in Emerald Lake in 1986 and 1987. Peterson and Schnabel mark-recapture estimates have large confidence limits, but we were able to obtain more precise population estimates in Emerald Lake during the spawning seasons in October and November. During the spawning season large numbers of Emerald Lake fish either congregate in the northwest and southeast corners of the lake or enter the outlet stream. Because we observed much larger numbers of trout in these aggregrations or migrant populations than while snorkeling, we could obtain more precise population estimates by comparing numbers of marked and unmarked fish in these populations.

Pond 2 was censused by the Petersen mark-recapture method (Ricker 1975) in 1986 and 1987; the fish were captured by seining. Pond 1 was censused in 1986 and 1987 by the Schnabel mark-recapture method (Ricker, 1975) using multiple fyke net sets.

Stream populations were estimated by the depletion method with three electrofishing passes and by the Petersen mark-recapture method. Confidence intervals for the depletion technique were calculated by the method of Zippin (1956). Pear Outlet in 1985 and Heather Outlet in 1985, 1986 and 1987 were so low by late summer that all fish could be removed and counted.

Underyearlings were too difficult to capture for adequate depletion or mark-recapture estimates, so we used direct counts to estimate their numbers. Snorkel counts were made in all 4 lakes in 1985, 1986, and 1987. Day and night counts from shore were made in Emerald Outlet all three years. Underyearlings in the ponds were counted both by snorkeling and by observation from shore, but the latter method was usually more practical because the ponds were often too shallow for swimming.

Fish Diet

Subsamples of adult fish captured by angling, electrofishing, or seining were stomach-pumped for diet analysis using a technique similar to Foster (1977) and Mehan and Miller (1978). Stomach contents were preserved in 70% ethanol. Underyearlings were too small for stomach pumping, so small numbers were killed and preserved in ethanol. Prey organisms were identified to the lowest practical taxonomic level, which was usually genus or species for common aquatic taxa.

Gonad Development and Fecundity

Samples of fish were removed for examination of gonads during the spawning seasons of 1985 and 1986 (all lakes) and again in 1987 (Emerald Lake). The pond and stream populations were not sampled regularly after gonads matured because we did not wish to reduce the small numbers of spawning females and disrupt normal spawning behavior. Gonads were removed and weighed to 0.01 gram, and ovaries were preserved in 70% ethanol or Gilson's fluid for later egg counts. We used only pre-spawning females for estimates of fecundity.

Behavior

The locations and depths of lake fish were recorded at the time of their capture. Locations were determined on grid maps of the lakes and depths were estimated as near-bottom, mid-water or surface. Adult and juvenile fish observed by snorkeling were identified if marked and their locations and group size were recorded. Spawning activites were observed with binoculars from vantage points around Emerald Lake and the outlet stream and ponds.

During the spawning runs in October and November 1985-1987 all 4 stream traps were checked twice daily. During periods when no fish entered the traps for several days, the frequency of checks was reduced to once a day or once on alternate days. Trapped fish were sexed, weighed, measured, marked for later identification and released. This gave us information on time required for spawning and weight changes during stream residency.

In 1987 we described at biweekly intervals the locations of a sample of underyearling trout in the lake, stream and Pond 1. Fish were observed for one to three minutes, then their distance from the bottom, surface and shore were measured with a meter stick.

Egg Deposition, Embryo Development and Embryo Survival

During the spawning season (October-November) the Emerald outlet was searched every 2-3 days for new nests. All nests were marked with flags. In 1985 each nest was assigned to one of four treatments. One set of nests was marked with a flag, excavated to confirm the presence of eggs, then reburied; a second set was excavated and the eggs were counted and reburied; the eggs from a third set were placed in 13 cm long by 7 cm diameter cylindrical boxes made of plastic mesh (Vexar, mesh size 3.8 X 3 mm). These cylindrical "Harris" boxes were then buried to the original depth of the nest (Harris 1973). The eggs from a fourth set of nests were placed in 10 X 15 X 5 cm plastic mesh boxes with 6.4 mm mesh. Six cubic modules, made of 3.8 X 3 mm mesh 5 cm on a side were placed in each of these boxes. Equal numbers of eggs were placed in each module, using a hose connected to a syringe, as the modules were filled with gravel. These "six-packs" were buried flush with the stream bottom. In 1986 and 1987 we did not use Harris boxes or the outer boxes in the six-packs. The individual cubes from the latter were buried independently.

Beginning the first week in November (1985) or January (1987, 1988) we removed a module monthly from each of the 9 (1985-86), 12 (1986-87), or 11 (1987-1988) six-packs. Modules were transported from Emerald basin on ice and examined in the laboratory (Ash Mountain or UCSB) within 16 hours. There was no evidence of mortality from these operations. In the laboratory, we inspected embryos for developmental stage and amount of mortality. At the time of hatching in 1986, which began during the first week in January, we placed Harris boxes and the remaining six-packs in emergence boxes made of 1 mm square mesh glued to 30 X 18 X 12 cm plastic frames. These boxes were provided with 1 mm mesh nets on the downstream ends to capture fry as they emerged from the gravel. In 1987 and 1988 we eliminated the emergence boxes and simply noted the developmental stage and survivorship of eggs and larvae in the six-packs.

Starting the first week of October in 1985 and 1986 we scanned Emerald Lake's inshore areas every few days for spawning fish or signs of previous excavation. These surveys were conducted by walking the lake's perimeter or by snorkeling. All nests observed by snorkeling were also visible from shore.

Just before the lake froze in both years we counted the number of depressions constructed by fish in the lake. In 1985 we excavated twenty-four depressions in the lake while wading or SCUBA diving; however, eggs were found in only two nests in the southeast corner and only four nests in the northwest corner. With the exception of three nests in very shallow water in the northwest corner, we attempted to rebury all eggs. Eggs from the three northwestern nests were placed in six-packs. Because of debris deposited by avalanches we were not able to recover these six-packs.

Amphibian Surveys

Amphibian populations in ponds near Emerald Lake were studied from late June/early July to September in 1985, 1986, and 1987. Ten ponds were surveyed for amphibian populations every two to three weeks in 1985. Fifteen ponds were monitored for amphibians at monthly intervals in 1986 and 1987. Two ponds in 1985, five in 1986, and four in 1987 did not contain amphibians. Depth and surface temperature were recorded from each pond on each survey date. Water samples for pH were taken on two dates about one month apart in 1985. Initially we attempted to measure pH of ponds in the field using a portable pH meter; however, we were unable to obtain stable pH readings so most samples in 1985 were transported to the Ash Mountain laboratory and pH was measured with a laboratory pH meter within 48 hours. Samples from two dates were likewise analyzed in the lab in 1986, and ANC was also measured. pH and ANC from 4 sample dates in 1987 were measured in the laboratory. In all cases, pond water was sampled after major snowmelt had ceased.

In 1985, tadpole population sizes for each pond were estimated by visual counts and by sweeping with a hand net (1 mm mesh). A sample of amphibian larvae (6 to 24 tadpoles/pond) was preserved in 95% ethanol for identification in 1985. Amphibian larvae were also measured and examined for physical abnormalities, and developmental stage was determined. Preserved specimens were identified according to Stebbins (1966). In 1986-87 we only noted the presence or absence of amphibian larvae in each pond on each sampling date.

Results

Fish Population Censuses

Emerald Lake contained about 1000 brook trout older than one year, and there was little change in population size from 1985 to 1987 (Table IX-2). There were 150 to 250 adult fish in Pond 1 and 200 to 320 in Pond 2. Despite wide confidence limits for population estimates, our calculations indicate that Heather and Aster Lakes each contained about 800 and 1200 adult fish, whereas we estimated approximately 660 adult fish in Pear Lake (Table IX-2). Pear Lake is heavily fished by the public and we estimated that approximately 300 adults were removed from the lake during the 1985 tourist season.

Young-of-the-year (YOY) counts were more variable from system to system and from year to year. High counts in 1985, 1986 and 1987 respectively were 242, 10 and 100 in Heather Lake, 262, 29 and 130 in Aster Lake, 932, 76 and 571 in Pear Lake, and 428, 67 and 323 in Emerald Lake (Table IX-2). We have designated the highest counts as best estimates in Table IX-2 because low counts in early summer were made before all fish had emerged and low counts late in the year may have been partly due to difficulty in locating schools of fry in mid-water. Poor recruitment in 1986 was probably due to unusually severe winter weather and a much later thaw than occurred in the other two years. No YOY were found in the Heather Lake outlet during the 3 years of the study, and only very small numbers were found in the Pear and Aster Lake outlets. In contrast, 198 YOY were counted in the Emerald Lake outlet in 1985, 26 in 1986 and 101 in 1987 (Table IX-2). Very few adult trout were found in the Pear and Heather Lake outlets.

For the Emerald outlet and Aster inlet and outlet streams Leslie regression (depletion) estimates were appreciably lower than our total seasonal counts (the actual number of fish captured and individually marked) or our mark-recapture estimates (Table IX-2). Originally we thought that this discrepancy was due to movement of unmarked trout from the first pond below Emerald Lake into the study section of the outlet, and to movement of marked fish from the outlet into the downstream ponds. However, trapping data from the summer of 1987 did not support this assumption. For example, eight fish left the stream during the night after a depletion census on 10 July, but none was a fish marked in the census. Between the original marking on 10 July and recapture operations on 14 September, only one of the 72 marked fish left the stream and only two unmarked fish entered from Pond 1. Clearly movements of this magnitude could not account for the two to fourfold differences we have seen between mark-recapture and depletion census results. We now believe that the depletion technique underestimates population size in the study streams. Probably catchability declined after the first pass because the fish entered deep cracks under boulders and entirely avoided the electric field. We conclude that well over 100 adult fish reside in this 100 meter stream, and 75 to 100 fish live in comparable stretches of Aster outlet and inlet.

Although recruitment of underyearlings is variable from year to year, our data indicate that populations of brook trout in Emerald Lake and associated waters (the outlet stream and ponds) remain relatively constant. Success of reproduction is probably related to local weather changes, whereas the constancy in adult populations is probably related to adult longevity and dominance by a few year classes (see below).

Age, Growth and Mortality of Fish

The size structures of trout populations in Emerald, Heather, and Aster Lakes were similar and unimodal in 1985, but few small fish (other than YOY, which were not collected) were found in Pear Lake (Fig. IX-3). Modal length of fish one year old or older was 180 mm in Heather and Pear Lakes, 175 mm in Emerald Lake, and 170-175 mm in Aster Lake. There was little month-to-month variation in the size structure of juvenile and adult trout in Emerald Lake during the summer and autumn (Figs. IX-4 through IX-6); however, the modal length of juvenile and adult Emerald Lake trout increased from 175 to 180 mm from 1985 to 1986 and from 180 to 185 mm from 1986 to 1987 (Fig. IX-3) The mean weight of Emerald Lake fish one year or older was 81.8 g in 1985, 79.4 g in 1986, and 78.8 g in 1987, giving an average standing stock of 31 kg/ha. In 1985 mean weights of juveniles and adults in Aster, Heather, and Pear Lakes were, respectively, 69.3, 86.1, and 100.9 g giving standing stocks of 45, 35, and 10 kg/ha (Table IX-3).

Fish in the study streams were generally smaller than those in the lakes (Fig. IX-7, Table IX-3). In some cases the size-frequency distribution for stream adult populations was distinctly bimodal. For example, in Emerald Outlet in 1985 there was a mode at ca. 95 mm and another at ca. 165 mm. In 1986 the modes were at 110 and 165 mm. In 1987 there was a small mode at 90 mm and a large peak at 140 mm (Fig. IX-8). Although the growth of YOY in the

Emerald outlet is obvious from size-frequency analysis, the size structure of the adult and juvenile populations remained relatively constant through the summer and autumn (Fig. IX-9).

Juvenile and adult fish in Pond 1 were similar to outlet fish in average weight (Table IX-3) and in their conspicuous year-to-year changes in size structure. However, fish over 175-mm standard length, which were frequently encountered in the stream, were nearly absent from both ponds (Fig. IX-10).

Fry emerged from the gravel at an average size of 20 mm and grew rapidly for the first few months (Fig. IX-11). In 1985, YOY emergence was over by the end of June, whereas fry emergence in 1986 lasted until the end of July. In 1987 fry emerged from mid-June to mid-July. YOY growth rate in the outlet stream was similar from year to year, although growth began later in 1986. In contrast, YOY in Emerald Lake and Pond 1 grew more slowly in 1986 than the other years, and 1986 fish ended the growth season at a smaller size (Fig. IX-11). Growth was in fact similar in all 3 habitats in 1986, whereas in 1985 and 1987 growth in Emerald Lake and Pond 1 (1987 data only) exceeded that in the stream (Fig. IX-12). These data indicate that Emerald basin underyearlings grow from 20 mm (Total Length) to abcut 50 mm during their first month of feeding, regardless of habitat or time of year. In favorable years, some fish in the lake grow to almost 100 mm before winter, whereas the Pond 1 and stream fish peak at 80 mm and 60 mm respectively.

In their second summer fish from the Emerald system averaged 85-100 mm Standard Length. Emerald Lake trout grow more rapidly than Emerald outlet trout through their first four years, but then level off at a size of about 180 mm (Table IX-4, Fig. IX-13). In contrast, Emerald outlet fish continue to grow through their sixth or seventh year, reaching a size of about 180 mm. The oldest fish collected from Emerald Lake was 10 years old and 185 mm long, and the oldest fish collected from the Emerald outlet was 7 years and 180 mm long. The longest fish collected from Emerald Lake and the Emerald outlet were 245 mm (age: 7 years) and 195 mm (age: 6 years), respectively.

There were small differences in the growth patterns of fish from different lakes (Fig. IX-14). In Pear and Emerald Lakes trout length leveled off at 180 mm after three or four years, whereas trout continued to grow through 5 or 6 years in Heather and Aster Lakes, reaching asymptotic sizes of 180 to 200 mm (Heather) or 190 to 210 mm (Aster). No trout older than 7+

years were collected from Heather or Aster Lakes, but one exceptional female in Pear Lake was over 11 years old (Standard Length = 355 mm).

Physical Condition of Fish

Fish in the Heather and Pear Lake systems were in better condition than those in the Emerald and Aster systems in 1985 (Fig. IX-15). Trout in the streams below Aster and Emerald Lakes had lower condition factors than those in the lakes themselves, and condition factors in all Emerald basin habitats were higher in 1985 and 1987 than in 1986 (Figs. IX-15 and IX-16). In 1985 condition factors of trout in Emerald Lake increased from July to October, reaching a peak of 1.76 (Fig. IX-17). In 1986, however, condition factors increased from July to August, reaching a peak of over 1.57, then declined through November. In 1987 trout condition factors in July were similar to those in 1985, but by August they were almost as low as in 1986. In the Emerald outlet mean condition factors remained relatively constant through the summer in 1985, increased from July to September in 1986, and declined during the summer in 1987 (Fig. IX-18). No trout were collected from the outlet after September because we wished to avoid disrupting spawning activities in the outlet stream.

Whole body lipid content in Emerald Lake fish abruptly declined as the trout spawned in October-December, and remained at low levels through the winter and spring (Table IX-5). There was a significant negative relationship between body fat and body-water content (Fig. IX-19). Lipid contents of trout collected from Heather, Pear, Aster, and Emerald Lakes in the autumn were fairly similar (7.5 to 12 % of dry weight), although there was a tendency for Pear Lake trout to have lower body-fat levels (Table IX-5; Fig. IX-20).

Reproductive Biology of Fish

In the Emerald system male trout first became reproductively mature at the age of 1 year, and females first matured at 2 years. Most fish were mature by age 3. The ratio of gonad-weight-to-body-weight (Gonadosomatic Index, GSI) of Emerald Lake females increased until early October in 1985 and 1987, but remained relatively constant through September in 1986 then increased until late October (Fig. IX-21). GSIs of lake males were highly variable but tended to follow the female pattern. As with condition factors, female GSIs and the numbers of eggs per ovary were higher in 1985 than in 1986 in all lakes (Figs. IX-22 and IX-23). In 1987 Emerald Lake females had GSI values and numbers of eggs/ovary similar to those in 1985. The diameter of eggs in ripe females was greater in 1985 than in 1986 in Aster Lake, but was comparable in these two years in Heather Lake (Fig. IX-24). The diameter of eggs was greater in Emerald than in Aster and Heather Lakes in 1986 (3.8 vs. 3.0 and 3.1 mm). In 1987, egg diameters were comparable in Pond 1 and Emerald Lake, but eggs were largest in the Emerald Outlet residents.

In 1985 nests were first found in the Emerald outlet on 2 October, and fish began migrating upstream from Pond 1 at the same time (Fig. IX-25). Migration from the first pond into the outlet peaked in the first week of October, but ripe pond migrants were trapped ascending into the outlet stream until early November. In 1986 reproductive adults began entering the outlet stream from Pond 1 on 26 September; however, gonadal development was delayed relative to 1985 and spawning was not observed until 14 October (Fig. IX-26). In 1986, pond fish continued to move intermittently into the outlet stream until 24 November. In 1987 spawning by resident stream fish began on 30 September, but there was virtually no flow for passage from the other habitats until 24 October. A large number of fish entered from Pond 1 during the week following 24 October, with lesser numbers entering until mid-November.

After a large precipitation event (45 mm snow water equivalent: Dozier et al. 1989) on 22 October 1985, a large number of fish migrated from Emerald Lake into the outlet study section (Fig. IX-25). In contrast, lake fish began entering the outlet on 30 September in 1986 and continued at a low rate until 25 November. In 1987 trout began entering the outlet from the lake on 25 October, again coincident with increased flows. All spawning in the outlet ceased by 21 November in 1985, 2 December in 1986 and 24 November in 1987. In each case the end of spawning appeared to coincide with the stream reaching 0°C.

Spent trout began moving from the outlet stream into the first pond after mid-October in 1985, late September in 1986, and late October in 1987. This movement continued through November in all years. No fish moved from the outlet into the lake in any of the years, probably owing to the shallow depth of a small waterfall connecting the lake and outlet stream.

In general, then, spawning and associated movements in Emerald Outlet extended from late September-early October through late November. Spawning migrations into the outlet from Pond 1 and Emerald Lake started earlier and were more sporadic and protracted in 1986 than in 1985 and 1987; however. actual spawning in the outlet started and stopped later in 1986 than in 1985. Earlier movement into the outlet stream in 1986 vs. 1985 and 1987 was associated with a higher discharge in early autumn in 1986. Discharge was low after mid-October in 1986 and few lake fish migrated into the outlet (Fig. IX-26). In 1985 and 1987, migration of fish from the lake to the outlet was spurred by rising water levels associated with storms which occurred after mid-October (Figs. IX-26 and IX-27). Spawning continued until temperatures approached 0°C.

In 1985 the sex ratio of fish entering the outlet stream from Pond 1 was always close to one, but in 1986 early migrants were primarily males and the majority of late migrants were females (Fig. IX-28). The overall sex ratio was close to one, with the males being slightly more numerous in both years. In 1987, females outnumbered males at first, but fish toward the end of the run were mostly males; the overall male/female ratio was higher than in the other years. The spawning runs from Emerald Lake into the outlet were rather different from the Pond runs in their details. In 1985 and 1986 males were somewhat more numerous in the first third of the runs, while females later outnumbered males. In 1987, males outnumbered females during most of the run.

Nest sites chosen by females were in areas with current speeds (measured one cm above the substrate surface) from 0 to 26 cm/s, although most velocities were less than 10 cm/s (Table IX-6). Velocities over nest sites were correlated with the velocities available: the stream was high during much of the 1985 spawning season, lower in 1986, and in 1987 the first spawners dug nests in still water. The respective average velocities over nests during the 1985, 1986 and 1987 spawning seasons were 10.2, 6.7 and 5.2 cm/sec. .

Eggs were deposited under about 4 to 11 cm of gravel covered by 12-13 cm of water. The number of nests in the outlet increased during the spawning season, reaching a peak of 54 in 1985, 56 in 1986 and 57 in 1987 (Fig. IX-29). The mean number of eggs per nest was higher in 1985 (54 eggs/nest) than in 1986 (44 eggs/nest), but was highest in 1987 (63 eggs/nest). According to our estimates, the number of live embryos in the outlet at the end of the spawning season was slightly higher in 1985 (2800) than in 1986 (2500), but was highest in 1987 (3600) (Fig. IX-29, Table IX-7).

Spawning was first observed in Emerald Lake on 14 October in 1985, 21 October in 1986, and 13 October in 1987. Spawning continued through lake freeze-up in all years (14 November, 1985, 17 November, 1986, and 23 November, 1987). Most spawning was concentrated in the northwest and southeast corners of the lake, the only areas having suitable substrates for spawning. Just before freeze-up in 1985 we counted approximately 130 to 160 depressions constructed by spawning females in the lake. Examination by a diver revealed that only about a third of these depressions contained eggs. From these observations we estimate that 50 viable nests, at most, were present in the lake by the end of the spawning season each year.

Eight Emerald Lake females dissected for gonad examination in 1985 produced an average of 298 eggs each (SE = 21), so the estimated 486 adult females spawning in Emerald Lake could have laid 145,000 eggs, assuming they spawn every year. In 1986 the fecundity of lake fish was much lower ($\bar{X}$ = 150 eggs/female, n = 18) and egg output for the 503 adult females spawning in the lake would have been 75,000 eggs. In 1987, average fecundity of 19 females was 281 (SE = 18), so the egg production by an estimated 428 females would have been 120,000 (Table IX-7).

A regression of egg number on female weight for 8 lake fish and 2 pond fish in 1985 produced the equation:

$$\text{Number of eggs/fish} = 90 + 2.03 \text{ (fish weight in g)}$$

According to this relationship, Pond 1 females, with an average weight of 45 g, produced about 181 eggs/fish in 1985. Although collection of females resident in the outlet would have disrupted spawning, we estimate from the average weight of adults (41 g, Table IX-3) that females produced 173 eggs each. Migrants from Emerald Lake were assumed to contain 298 eggs/female. The fish from Pond 2 produced an estimated 143 eggs each. In 1985 we estimate that about 193 females spawned in the outlet, including 53 from Emerald Lake, 3 from the lower pond, 47 from the upper pond, and 90 from the resident stream population (based on mark-recapture estimates).

Because the ratios of 1985 to 1986 fecundity for Emerald, Heather, and Aster Lakes were all approximately 2, we estimate that about 91, 87 and 149 eggs were produced by each pond, outlet and lake female, respectively, in 1986. In 1986 we observed 34 females from Emerald Lake, 58 from Pond 1, and 111 resident females spawning in the outlet, for a total of 203 spawners.

In 1987 we counted 83 females from Emerald Lake with an estimated 281 eggs/female and 68 from Pond 1 with an estimated 195 eggs/female. We estimate that there were already 95 females in the stream with 173 eggs each, for a total of 246 spawners.

Using the number of females spawning in the outlet each year and the number of eggs produced per female, we calculate that 40,000 eggs were laid in the Emerald outlet in 1985, 20,000 in 1986, and 53,000 in 1987. Adult females in Pond 1 primarily entered the outlet stream to spawn, but most females in Pond 2 remained there during spawning season. We estimate that the 109 adult females in Pond 2 produced a total of 16,000 eggs in 1985 and 8,000 eggs in 1986 (Table IX-7). Because of the lack of suitable spawning gravels in Pond 2, it is unlikely that many of these eggs survived the spawning season.

Combining the lake and stream results, we estimate that 200,000 eggs were produced by trout in the Emerald Lake system during the 1985 spawning season, 100,000 were produced in 1986, and 200,000 in 1987. In summer 1986 there were only about 67 fry in the lake, another 64 in the outlet and Pond 1, and 3 in Pond 2 for a total of 134 YOY. In 1987 there were 323 fry in Emerald Lake, 152 in the outlet and Pond 1, and 12 in Pond 2 for a total of 487. In 1988 there were 295 fry in Emerald Lake, 489 in the stream and Pond 1 and none in Pond 2 (Table IX-7). These calculations indicate that only 0.07%, 0.5% and 0.4% of eggs produced in 1985, 1986, and 1987 respectively, survived to the fry stage in the succeeding summers.

The high mortality of early trout stages can be attributed to the following sources:

1. Failure of females in the lake, stream or pond to deposit some or all of their eggs, or low fertilization success. We have reason to believe that this was a minor problem. Continual digging was observed in the lake from the beginning of the spawning season until lake freeze-up, and undoubtedly continued under the ice. As females do not defend nests after they bury their eggs, subsequent spawners utilize the same gravels as their predecessors. This insures that habitat is always available for spawning. More direct evidence comes from the recapture of marked pond and lake fish when they entered Pond 1 after spawning in 1985. The average ratio of gonad to body weight for 8 lake females and 2 pond females was 12.3% (SE = 1.1%) before spawning, which is nearly equal to the amount of weight lost by 11 tagged females during spawning (average weight loss = 17.2%, SE = 1.9%).

Nearly 98% of eggs excavated directly after deposition were viable, indicating that fertilization success was high.

2. Egg cannibalism. On 7 November 1985, we observed a female spawning in the northwest corner of the lake. Before this female could cover or defend her nest several males began eating her eggs. Evidently the eggs were all consumed, because she did not cover the nest afterwards. In 1986 we observed five spawning lake females for a total of five hours. All eggs produced by these females were eaten by intruding males. In excavating over 20 nests in 1985 we found that only seven contained eggs. Although we did not concentrate on spawning localities when sampling trout for diet in the lake, we found trout eggs in 2 of 5 fish examined during the spawning period in 1985. Of 5 fish taken in Heather Lake on 3 October, 1986, 1 contained eggs. Similarly, on 1 October 1986, 1 of 5 fish from Aster Lake contained 30 eggs in addition to 2 underyearling trout.

3. Use of gravel by successive females. Lake females were observed reworking the same gravel for more than a month, and any exposed embryos were probably consumed. Nest destruction by subsequent spawners, termed "superimposition", was also common in the outlet stream. Nearly all of the plastic flags used to mark nests were dug up, knocked down or buried several times during the spawning season. Inspection of the disturbed nests indicated either removal of the gravel (and embryos) to cover a nest downstream, or the placement of new eggs in approximately the same location. Loose eggs were found on the stream bottom on several occasions.

We estimated fewer than 50 viable nests in the lake during the entire spawning period in 1985, and the three nests we were able to excavate contained an average of 45 eggs each. Therefore 2,250 viable embryos would be an upper estimate of the number of embryos present in the lake after spawning had stopped. If we assume that a similar number of embryos was left at the end of the 1986 and 1987 spawning seasons, this means that only 1.5, 3 and 1.9% of the eggs deposited in the lake in 1985, 1986 and 1987, respectively, survived to the end of the spawning season.

Substrate suitable for spawning in the outlet stream is insufficient for all of the females that spawned there. We confirmed only 54 active nest sites in 1985, 56 in 1986, and 57 in 1987. Given the average number of eggs per nest, we calculated that 2,900 eggs were present at the end of the spawning season in 1985, 2,500 eggs in 1986, and 3,600 in 1987. Given that 40,000 eggs were laid in the outlet in 1985, 20,000 in 1986, and 53,000 in 1987, ca. 87 to 93 % of the eggs laid in the outlet were destroyed by spawning activities (Table IX-7). This amounts to the destruction of 741 nests in 1985, 455 in 1986, and 714 in 1987. Because lake fish were the last to arrive, particularly in 1985, their embryos might have suffered less mortality. Although we have no estimates of viable embryos present in Pond 2 in December, recruitment to the Pond 2 population has been very low in the three years that we have estimates. In general, then, more than 95% of eggs in the Emerald Lake system were lost to superimposition and cannibalism.

4. Poor survival of late embryos, and sac fry. Survival was high through hatching in 8 of 9 six packs in 1985-86 (Table IX-8). Results from the nest constructed on the last spawning date (21 November, Nest 52 in Fig. IX-30) indicate that few of these eggs were viable, probably owing to lack of fertilization. Because few nests were constructed near the end of the spawning season, survivorship in the first eight six-packs is probably more representative of embryo survival for the population. These data indicate that embryonic mortality was low to February.

When eggs from the first five six-packs hatched in January, 1986, we transferred the modules into emergence boxes. The other three six-packs, which were located in the upper part of the outlet, were left in place because they did not hatch until late spring.

An unusual event in February 1986 may have contributed to the mortality of sac fry and embryos in the natural stream environment. At this time a large avalanche occurred in the Emerald Lake basin. This avalanche hit the ice-covered lake, causing an abrupt rise in water level. A large volume of water rushed out of the lake through the outlet channel, and snow and logs in the outlet were moved by flood waters. Although our egg baskets and emergence traps were moved, we were able to recover nearly all of them. Two of our baskets, however, were crushed, and the rest were filled with silt or fine sand. The natural substrate in the stream was redistributed, and most nests were covered by sand or fine sediment or were washed away. Survival of embryos was high (>75%) in the 3 boxes outside of emergence containers (until early May, when the last of the modules was removed), perhaps because the boxes were located near the lake outlet where less deposition of debris occurred. Although we planned to count fry in the emergence boxes as they emerged into downstream nets, only two fry were found before high flow terminated this experiment in late May. A few dead sac fry were found in the nets, and many dead and decaying eggs and sac fry were found in the boxes after flooding occurred. Only 0 to 20% of eggs or sac fry found in boxes were alive. The results for Harris boxes paralleled those from the emergence boxes. These observations indicate that mortality of embryos was approximately 80-100% in all emergence boxes. Because of high pre-emergence mortality we could not determine the success of actual emergence.

Because of low stream flow, scant snow cover and low temperatures in 1986-87, much of the gravel in the lower portion of the stream froze solid. Mortality of embryos was virtually 100% in this area. In January 1987 ten of 12 "six-packs" contained live embryos, but by February only four experimental nests could be removed from the ice. Examination later in the winter indicated total mortality of the embryos that froze. In two of the 4 nests that could be removed, only 5 of the original 88 embryos were found alive from February to May, and none were alive in June. The cause of mortality in these two nests is unknown, although it occurred during the same period as the ice-related deaths (Fig. IX-31). The only live embryos were found close to the lake where they received slightly warmer water.

In the 1987-88 development season yet another natural catastrophe occurred. The stream temporarily stopped flowing early in the spawning period, and one of the experimental nests (Nest 1, Fig. IX-32) dried and was twice disturbed but not destroyed by some type of scavenger (probably a pine marten). Although all of the embryos in the nest were dead by January, we could not determine if they were killed by drying or by agitation. A similarly de-watered control nest nearby contained live embryos in the damp gravel, but it was also in a shaded spot and was not disturbed. All of the embryos in a second experimental nest died between October and January, but we do not know if this mortality was related to cessation of flow. All of the eggs in the last nest of the season died as they did in 1985, presumably due to lack of fertilization. Survival in most of the remaining nests was high to at least 5 June, at which time an average of 56% (range 0-93%) of the original embryos remained alive in the six-packs or had escaped through the mesh as sac fry prior to removal of the boxes. Fry counts later in the summer revealed, however, that only 14% of the original viable embryos survived, so emergence from the gravel must have been relatively unsuccessful (about 25%). Even so, fry recruitment in 1988 was better than in either of the other study years (7x 1986 and 3x 1987 levels, Table IX-7).

To summarize, the percentage of embryos surviving in the outlet from the end of spawning season to egg hatching was 86% in 1985-86, 13% in 1986-87, and 39% in 1987-88. By the end of emergence, the proportion of original embryos still surviving (i.e, as live fry) dropped to 2% in 1986, 6% in 1987 and 14% in 1988. During the first season, most mortality occurred after hatching; during the second season, mortality occurred after the end of the spawning season but before hatching; in the third season, most mortalities probably took place early in the spawning season, with further losses occurring during emergence. The timing of embryo or fry mortality was determined by weather events: the number of embryos and fry was drastically reduced by a February flood and high spring discharge in 1986, and by interstitial ice formation in 1987. In fall 1987 the stream stopped flowing during part of the spawning season, and disappeared completely in some areas. An unusual amount of silt was deposited on nests where water remained, probably decreasing survival late in development. The result of weather-related differences in embryo survival was great year-to-year variability in numbers of YOY counted in the Emerald system. Maximum counts were >600 in 1985, <200 in 1986, about 500 in 1987 and about 800 in 1988.

In 1985-86 development rates of eggs were greatly affected by rapidly declining water temperatures in the autumn (Fig. IX-30). Temperatures dropped from 15 to 5°C from the first of October to mid November. Eggs laid in early October when water temperatures exceeded 8°C took about 100 days to hatch. In contrast, eggs laid in early November during a rapid temperature drop (7.5 to 1.5°C) began hatching after 180 days. Since they were deposited almost a month later, the November eggs hatched three to four months (January vs. April-May) after the earliest broods. The earliest broods had begun emerging from the gravel by mid-April but live sac fry were found in one Harris box as late as 15 July. In 1986-87 the few eggs not destroyed by ice began hatching in late April-early May (Fig. IX-31). Because embryos in most boxes were destroyed by freezing and hatching was drastically delayed relative to 1985-86, there were once again insufficient modules in six-packs to follow embryo development through fry emergence. No YOY were observed in the stream through late June, and no fry were captured in drift nets set in the outlet stream in early May and early June, 1987.

Food habits

Numbers of prey per stomach in Emerald Lake trout increased after July and began declining later in the summer (Figs. IX-33 and IX-34). Because digestion rates are lower in colder water (after September in Emerald Lake), these results indicate that consumption rates peaked in August or September. Feeding of adults in 1985 was evidently more variable among individuals and higher on the average than in the other years, primarily because some individuals fed on large numbers of cladocerans. Because these organisms are so small compared to most other prey, this difference among years may not have been nutritionally significant. Underyearlings contained fewer prey on the average than adults in all months for which we have data, except September and October of 1987.

Prey numbers per trout stomach in the other study lakes were generally higher in October than in July. Mean numbers were higher in 1985 because some individuals contained large numbers of organisms. (Fig. IX-35). None of the lake fish sampled in three years of study had an empty stomach

Summer and autumn trout diets in Emerald Lake were dominated by chironomid pupae and larvae, cladocerans, and terrestrial insects (Fig. IX-36). Expressed as a percentage of total prey items in trout stomachs, terrestrial arthropods dominated trout diets in July and October of 1985 and 1986, whereas cladocerans dominated trout diets in August, September, and November of 1985, September of 1986 and October of 1987 (Fig. IX-36). Relatively few chironomids were eaten in 1985, but they were numerically important in mid-summer diets in 1986 and 1987. The percentage of trout stomachs containing terrestrial arthropods declined from July to September then increased until November in 1985 and 1986, but no such pattern appeared in 1987 (Fig. IX-37). With the exception of July-August, 1986, cladocerans were always found in a high proportion of trout stomachs (>40%) (Fig IX-37). Chironomid larvae and pupae were always present in >40% of trout stomachs except for September 1985 and 1987 (for larvae) and October 1985 and 1987 (for pupae). The dominant cladoceran taken after July in 1985 was Daphnia rosea, whereas Eurycercus lamellatus was the major cladoceran eaten in September-October 1986. In 1987, Eurycercus was more important than Daphnia in July, but Daphnia was more important in September and October (Fig. IX-38). Limited quantitative data indicate that fingernail clams (Pisidium) and chironomid larvae are the most important components of trout diets in the winter and spring, when the lake is ice-covered (Table IX-9).

Stomach contents of adult fish in the other lakes were numerically dominated by cladocerans and terrestrials in 1985 (Fig. IX-39). In July 1985, most of the major prey groups (chironomid larvae and pupae, cladocera, acarina, trichoptera and terrestrials) were found in most of the adult trout, but by October only cladocera were found in the majority (Fig. IX-40). Diets were similar in October of 1986, but chironomids, cladocerans and terrestrials were found in a larger proportion of the individuals sampled (Fig. IX-41).

YOY diets in Emerald Lake were dominated by cladocerans in 1985, by cladocerans (size class 0-50 mm) or chironomid larvae (51-100mm) in 1986 and by chironomid larvae (0-50mm) or cladocerans (51-100mm) in 1987 (Tables IX-10 through IX-12). In 1985, 1986 and 1987, fish 101-150 mm in standard length ate predominately cladocerans. For trout 150-200 mm in length the largest dietary components were cladocera in 1985, cladocera and chironomid larvae in 1986 and cladocera and chironomid pupae in 1987. Terrestrial organisms ranked a distant second in 1985 and third in 1986 and 1987 (Tables IX-10 through IX-12). The largest fish (>200 mm SL) ate predominately terrestrial arthropods (1985) or a combination of terrestrial arthropods and chironomid larvae and pupae (1986). In 1987 they ate mostly terrestrial arthropods with lesser numbers of chironomid pupae and water mites (Acarina). In general, the importance of terrestrial arthropods increased in the diet of older, larger fish, whereas cladocerans were most important to fish 100 to 200 mm in length and cladocerans or chironomid larvae were most important to YOY's (0-100 mm). Cladocerans are among the smallest and terrestrial insects among the largest of prey items taken. Chironomid pupae were observed in YOY diets in 1985 but were rare in the diets of older fish, whereas in 1986 the importance of chironomid pupae in trout diets increased with increasing trout size. In 1987 chironomid pupae were moderately important in all size groups (Tables IX-10 through IX-12). The number of prey per stomach tended to increase to intermediate trout sizes (51-200 mm SL) then decline for the largest fish (>200 mm SL). For fish 100-200 mm in length there were more items per stomach in 1985, when diets were overwhelmingly dominated by cladocerans, than in 1986 and 1987, when much larger chironomids and terrestrial arthropods were more important (Tables IX-10 through IX-12).

Although there were general trends in trout diet with changes in season, year, or trout size, fish taken on the same day in the same part of Emerald Lake were highly variable in their diets. For example, on 9 July 1985, we captured 7 fish of similar size at one spot in the northwest corner of the lake: 5 near the bottom and 2 at the surface. Of the five bottom fish, four contained almost exclusively clams or benthic invertebrates, while one contained a mixture of benthic and terrestrial species. One surface-caught fish contained a mixture of terrestrial and benthic species, but the other had eaten nearly all terrestrial prey. On another day, 30 August 1985, large numbers of winged ants were flying over the lake, and 4 of 9 fish contained 26, 109, 165, and 240 ants in addition to other terrestrial insects and spiders. Three of the 4 were caught at the surface and one at approximately midwater. Another 4 out of the 9 contained predominantly chironomid pupae; three were caught at the surface and one at midwater. The ninth fish contained chironomid pupae and a large number of Daphnia, and was caught at midwater.

In the Emerald Lake outlet the number of prey in adult trout stomachs declined from July through September in both 1985 and 1986, and the number of prey per stomach was higher in 1986 than 1985 (Fig. IX-42). Stream fish generally contained fewer prey items than Emerald lake fish at comparable times (Figs. IX-33 and IX-42). Mean numbers of prey in underyearling stomachs showed little temporal variation (Fig. IX-43). Stream YOY did not contain consistently fewer prey than lake YOY. Diets in the outlet were more diverse than in the lake, and were dominated by terrestrial arthropods, chironomids, simuliids, trichopterans, ephemeropterans and plecopterans in 1985 and terrestrial arthropods, chironomids, simuliids and trichopterans in 1986. In 1985 no one prey taxon composed more than 40% of prey items found in trout guts, but in 1986 simuliids contributed more than 60% of the diet in July and August and chironomids numerically dominated diets in September (Fig. IX-44). Terrestrial arthropods and chironomid larvae were found in a high proportion of trout stomachs through the summers of both years (Fig. IX-45). In 1986, almost all trout stomachs contained both types of prey. The proportion of trout stomachs containing simuliid and trichopteran larvae declined from early to late summer, and was higher in 1986 than 1985. In contrast, the proportion of stomachs containing stonefly (Plecoptera) and mayfly (Ephemeroptera) larvae was often less than 0.40, and was often higher in 1985 than 1986 (Fig. IX-45). Simuliid larvae and terrestrial arthropods were the most abundant items found in the stomach of one outlet trout collected in the winter (Table IX-9). We do not have enough 1987 data for adult diet analyses comparable to those above. Two stomachs from 10 July contained chironomid larvae, a few other aquatic insects and some terrestrials. One stomach from 6 October contained cladocerans; another contained cladocerans and a trichopteran.

In 1985, the diet of outlet trout up to 50 mm SL was numerically dominated by chironomid larvae (Table IX-13). Simuliid and chironomid larvae were the most abundant items in diets of trout 51-100 mm in length, whereas terrestrial arthropods were the most abundant items in the diets of larger fish (>100 mm). Similarly, in 1986 the smallest fish consumed mostly chironomid larvae, while 51-100 mm fish ate mostly chironomid larvae, simuliid larvae and terrestrial arthropods (Table IX-14). Larger fish ate mostly simuliid larvae in 1986. In 1987, small fish (<100 mm) ate primarily cladocerans and chironomid larvae (Table IX-15).

To summarize, the proportion of chironomid larvae in Emerald outlet trout stomachs decreased with increasing fish size during all 3 seasons (Tables IX-13 through IX-15). Representation of terrestrials increased with fish size in 1985, but not in 1986. Simuliid larvae were an important component of diets of trout >50 mm long in 1985 and 1986. Other aquatic taxa commonly found in the stomachs of trout >100 mm SL in 1985 included the larvae of chironomids, mayflies, stoneflies, and caddisflies. Chironomid and caddisfly larvae were also important components of trout diets in 1986 (Table IX-14).

October was the month of most intense YOY feeding in Pond 1, both in 1986 and 1987 (Fig. IX-46). As in Emerald Lake and its outlet stream, chironomid larvae and cladocerans were the most important food for YOY in the pond (Table IX-16). Eurycercus was more important than Daphnia in nearly all samples.

Behavior of Underyearling Fish

The physical habitats of underyearlings in the lake, stream and pond changed with time during the 3 summers of our study. As they grew older, YOY in Pond 1 and Emerald Lake moved from the shallows into deeper water offshore (Figs. IX-47 and IX-48). Fish in Emerald Lake were found at an average distance of 23 cm from shore and in water depths of 15 cm in July, but had moved to a mean distance of 108 cm from shore and 78 cm of water by 18 August. Fish in Pond 1 were initially found at a mean distance of 28 cm from shore and in 12 cm water and moved to an average distance from shore of 201 cm and 49 cm water depth during this same period. Emerald outlet underyearlings similarly changed to greater depths from July to August but were already in the deepest available positions by August.

When they were first observed in early summer, Emerald Lake YOY were primarily solitary and within 5 cm of the bottom. As the seasons progressed, a significant proportion of the fish joined schools and became more mobile. On 6 August 1986, for example, 94% of the YOY counted were solitary and 6% in pairs. Ice still remained in the lake at this time and emergence from the gravel had just been completed. By 3 September, only 62% were solitary and the remainder were in schools of up to 5 individuals. Similarly, on 10 June 1987 (a year when ice-off occurred over a month earlier than in 1986), 87% of the YOY were solitary and the rest were in small groups. By 4 August, only 47% were solitary and the remainder were in small schools. On 13 September, we observed a school of at least 50 individuals (about 15% of the year class) feeding on plankton in the southeast corner of the lake. The decline in number of fish counted after August (Table IX-2) may have been due to the movement of these large schools into open water where they were more difficult to locate.

Amphibians

Only two amphibian species were found in our study area. Tadpoles of the Pacific Treefrog (Hyla regilla) were found in eight of ten ponds surveyed in 1985, ten of fifteen surveyed in 1986, and eleven of fifteen monitored in 1987. In addition, treefrog tadpoles were collected in Topaz Lake. Of these ponds and lakes only Hidden Pond contained fish; however, adult Pacific treefrogs were also observed on single occasions in Emerald and Heather Lakes in 1985 and treefrogs were heard chorusing near Aster, Emerald, and Heather Lakes. The Mount Lyell Salamander (Hydromantes platycephalus) was sighted on 29 August 1986 by Michael Williams on the Watchtower Trail and on 2 August 1987 by Frank Murphy near Alta Peak. Although the Mountain Yellow-legged Frog (Rana muscosa) is found at similar sites throughout the Sierra Nevada, it was not seen in the vicinity of Emerald Lake.

As evidenced by mating vocalizations, Pacific Treefrogs emerge near the end of, or shortly after, snowmelt. Mating and egg laying occur soon thereafter. Our observations indicate that approximately one to two weeks elapse between egg fertilization and hatching. For example, a pair of treefrogs in amplexus was observed in Storage Tent Pond in mid-July 1986, and newly-hatched tadpoles were seen in the same pond in early August. Tadpoles developed for four to eight weeks before metamorphosing to the adult stage.

Larval size and rate of development varied from pond to pond and from year to year. On 9 July 1985, four ponds at low elevations (<2900 m) contained tadpoles varying in average snout-to-vent length from 10 to 18 mm (developmental stage VI to XV, Balinsky 1981). In contrast, the tadpoles in two high-elevation ponds (>3100 m) varied in average length from 7 to 9 mm (developmental stage II to IV). Tadpoles in the low-elevation ponds tended to be larger and more developmentally advanced than those in the high-elevation ponds through the rest of the season. However, some of the high-elevation populations had about the same size distribution as low elevation populations by the end of August, indicating that tadpoles in some of the high-elevation ponds developed at a faster rate than tadpoles in the low-elevation ponds. Two low-elevation ponds had dried by early August.

Snowmelt finished by June in 1985, and a few of the ponds surveyed were dry by July. In 1987 many of the ponds surveyed were dry by early July. In 1985 and 1987 most larvae had metamorphosed between the end of July and the end of August. In contrast, snowmelt was much later in 1986, ice remained on Emerald Lake until August, and ponds contained water later in the season. As expected, the late snowmelt and low temperatures in 1986 resulted in delayed egg laying and development. Tadpoles were not observed until the beginning of August in 1986, nearly a month later than in 1985 or 1987. In 1986 metamorphosis occurred between the end of August and the end of September.

The occurrence of larvae in ponds appeared to be unrelated to pond size, degree of permanence, elevation, or pH (Tables IX-17 and IX-18). The pH of ponds which contained tadpoles varied from 5.3 to 7.2 (mean, 5.9), whereas the pH of ponds rarely containing or without tadpoles varied from 5.7 to 7.0 (mean, 6.2) (Table IX-18). Acid neutralizing capacity varied both seasonally and between ponds on sampling dates. The only variable that appeared to be related to the occurrence of tadpoles was degree of exposure. Ponds that did not contain tadpoles tended to be heavily shaded by surrounding mountains or vegetation.

Tadpole population densities for 1985, the only year for which we have density data, varied from 0 to over 50 per m^2. Again, there appeared to be little relationship between tadpole density and pond size, degree of permanence, elevation, or pH. Two small (<25 m^2) ephemeral ponds, one at high (>3100 m) and one at low (<2900 m) elevation, had high tadpole densities in early July (40-55/m^2) which declined rapidly to low densities (ca. 1/m^2) by mid-July or late August. Most other ponds containing tadpoles had densities <20/m^2. Densities of tadpoles in Hidden Pond, the only pond containing fish, were especially low (< 12 in the entire pond). There was some consistency in the abundance of tadpoles among ponds across the three years of the study. Ponds which contained high densities in one year tended to have high densities in other years, whereas other ponds contained low densities of amphibians in all years.

Catastrophic events often caused extensive tadpole mortality. For example, tadpoles in two ponds died from desiccation by 8 August 1985. Similarly, in 1987, an exceptionally dry year, all of the tadpoles in three ponds died of desiccation by late June or early July. On 22 October 1986, hundreds of larvae and froglets died in Why Pond, the highest pond studied (3158 m elevation). This mortality was presumably caused by an early ice cover which deprived them of oxygen.

Two of 97 tadpoles examined in 1985 had physical abnormalities. One tadpole had a deformed (clubbed) hind foot and an unpigmented individual lacked one eye.

Discussion

A variety of population responses have been observed for fish and amphibians in parts of the world affected by cultural acidification. These include declines in population size, altered age and size structures, changes in individual growth rates and mortality schedules, and recruitment failure. In extreme cases aquatic vertebrate populations may be eliminated by acidic inputs. Because of vertebrate responses to acidification, aquatic vertebrate populations can act as sensitive indicators of the status of freshwater systems. Because the responses of freshwater organisms to acid stress are dependent on the chemistry of receiving waters, the buffering capacity of affected watersheds, and the genetic composition of animal communities, the effects of acidification will vary from region to region.

Unfortunately, there is little detailed information on fish and amphibian populations in the High Sierra. Although acid deposition is known to occur in these mountains, it is not known if episodic acidification currently has any effect on freshwater vertebrate populations. To determine trends in the population characteristics of fish and amphibians it is necessary to have long-term data sets. Long-term patterns may be obscured by natural interannual variation in measured parameters, but trends can be distinguished against the background of natural "noise" if "baselines" are long enough. Long-term data sets will also allow scientists to determine at what times, and to what extent, aquatic systems are being affected by anthropogenic inputs. The purpose of our investigations was to measure and describe population and other biological characteristics of fish and amphibians in a representative High Sierra system, i.e. lakes and streams in the Marble Fork of the Kaweah River basin. Because of the large amounts of time and effort needed to conduct detailed investigations of fish and amphibian populations, our efforts have been focused on Emerald Lake and its outlet stream, the study site used by the CARB for its Integrated Watershed Study. By comparing our data with literature data we can draw tentative conclusions regarding the current and potential effects of cultural acidification on freshwater habitats in the High Sierra. Our baseline data, which have been collected from 1985 to the present, also allow us to assess the extent of interannual variation and act as a benchmark for comparisons to future investigations.

In the following summary we will describe the behavioral and demographic characteristics of aquatic vertebrate populations in the Marble Fork basin, and describe the degree of and possible reasons for interannual variation. We will also compare our data to published accounts of population characteristics of these or similar species to determine how similar our vertebrate populations are to those in other systems. Finally, by comparisons with literature data we will provide some assessment of the impacts of episodic acidification on High Sierra fish and amphibians.

The study lakes contain reproducing populations of brook trout, Salvelinus fontinalis. The brook trout is fairly tolerant of high acidity. Although brook trout are occasionally found in waters as acidic as pH 4.1 (reviewed in Robinson *et al.* 1976), they are usually absent at pHs <4.7. Some mortality of the vulnerable early life stages may occur at pHs as high as 6.5 (Menendez 1976). Brook trout have been widely stocked throughout the High Sierra because they thrive in cold, dilute high mountain lakes and do not require running water for successful spawning. These habitats are coincidentally quite sensitive to acid inputs, so the brook trout is at unusual risk of acid effects despite their moderate tolerance of low pH.

Population sizes of adult brook trout in Pear, Aster, Emerald, and Heather Lakes were similar, varying from approximately 650 in Pear Lake to approximately 1200 in Heather Lake. Because of differences in lake areas, fish densities were more variable, ranging from 98 fish and 10 kg/ha in Pear Lake to ca. 650 fish and 45 kg/ha in Aster Lake. Changes in the density of juvenile and adult trout in Emerald Lake from 1985 to 1987 were slight. The small outlet ponds below Emerald Lake had trout densities greater than in the lakes (55-120 kg/ha).

Comparisons with literature data from trout lakes indicate that these standing crops are very high, particularly for such oligotrophic systems (reviewed in Carlander 1955, Saunders and Power 1970). Similarly, the density and biomass of fish in the Emerald outlet (362-472 kg/ha) were higher than those reported in the literature (25-230 kg/ha; O'Connor and Power 1976, Elwood and Waters 1969, Hoopes 1975, Power 1980). Density and biomass of brook trout from Marble Fork lakes and streams are similar, however, to those of lightly exploited Sierra systems, and may be typical of stunted populations (Deinstadt et al. 1985a and 1985b, McEwan et al. 1986, D.L. Hall personal communication).

Numbers of young-of-the-year were highly variable, ranging from 240 in Heather to over 900 in Pear Lake in 1985 and 10 in Heather to 80 in Pear Lake in 1986. These data indicate that YOY can comprise very small (1%, Heather 1986) or substantial (58%, Pear Lake 1985) proportions of total population numbers in these lakes. Spawning apparently occurs in October and November in all study lakes, and in the outlets of Emerald, Aster, and Pear Lakes and the inlet to Aster Lake. Few or no YOY were found in the outlet streams of Heather, Aster, and Pear Lakes; however, 200, 26 and 101 YOY were counted in the Emerald outlet in 1985, 1986 and 1987 respectively. Fry production in these lakes and streams is probably limited by the availability of suitable spawning gravels, and controlled within these limits by year-to-year changes in weather patterns (see below).

Growth of YOY in their first few months was comparable to that reported from other systems; however, YOY size at the end of summer was often smaller because the growing season was very short (Carlander 1969, O'Connor and Power 1976, Saunders and Power 1970). Most YOY emerged from the gravel in late June to early July in 1985 and 1987, and in late July to early August in

1986. Because of earlier emergence, YOY were larger at the end of the summer in 1985 and 1987 than in 1986. Growth in the first two years was within the range of values observed for other systems; however, growth rates declined to low values when fish reached three years of age, coinciding with the age at which nearly all fish were reproductively mature. Lengths of trout increasingly diverged from lengths reported in the literature as trout aged beyond 3 years (Donald et al. 1980, Carlander 1969, O'Connor 1976, Power 1980), but were typical of stunted brook trout populations in High Sierra lakes (Hall 1988). These data indicate that trout were allocating most of their energy to reproduction and maintenance rather than growth after they reached maturity.

Although Power (1980) indicates that brook trout rarely live beyond 4 years, many of the trout collected in our systems were >4 years old. A few individuals in Pear and Emerald Lakes were over 10 years old. The populations in our systems were dominated by old, small fish. For example, modal length (SL) of fish in Emerald Lake was 175 to 180 mm and most fish this size were 4 to 6 years old. Few fish over 200 mm SL were collected from the lakes and streams in the Marble Fork basin. Similar size and age structures have been reported for brook trout populations in other High Sierra lakes (Zardus et al. 1977, Hall 1988). As in most systems, the density of brook trout was greater and average individual body size was smaller in streams than in lakes. Juveniles and adults in the Emerald outlet population exhibited a bimodal size distribution in 1985, with modes at 100 mm SL (age = 1-2+ yrs.) and 165 mm SL (age = 5-6+ years). Because one- and two-year old fish were common in the stream but not in the lake, it is possible that these fish move into the lake as they grow older. However, fry counts in the lake indicate that reproductive success is roughly comparable in both habitats, so delayed migration to the lake might not fully explain the scarcity of yearling fish.

The condition of fish in the study waters was similar to that reported for trout populations described in the literature (Carlander 1969). Body-lipid content was closely tied to the reproductive cycle, peaking at the time of spawning then declining to low winter and spring levels (Nelson and McPherson 1987). When corrected for fish size, fecundities of females in lakes in the Marble Fork basin were similar to those reported in the literature (Power 1980, Carlander 1969, Saunders and Power 1970, McFadden et al. 1967), particularly for waters exhibiting low productivity (Nelson and McPherson 1987). The generally lower fecundities found in the Marble Fork lakes relative to those reported in the literature can be attributed to the smaller size of adult females in the Marble Fork systems. Condition factors, gonad-weight to body-weight ratios, and fecundity were all higher in 1985 than 1986, probably due to differences in the length of the growing season in these two years. Ice-out on the lake and snowmelt occurred approximately a month earlier in 1985 than in 1986. The weather situation in 1987 was similar to that in 1985, but condition factors of Emerald Lake fish were significantly lower in 1987 than in 1985.

As in most systems, brook trout spawned in October and November. Both resident stream fish and fish from Emerald Lake and the downstream ponds spawned in the Emerald outlet. Spawning movements were often tied to changes in water level, and were much more protracted and sporadic in 1986 relative to 1985 and 1987. The sex ratio of spawners from Pond 1 was always about 50:50 in 1985, but males moved into the outlet stream before females in 1986. In 1987 the sex ratio of early pond spawners was about equal, but the last third of the run was mostly males. The sex ratios in runs from Emerald Lake were remarkably similar in 1985 and 1986, with males slightly outnumbering females in the first third of the run and females outnumbering males for the rest of the run (and overall). The 1987 run was different, with males slightly more abundant than females throughout.

Because average fecundities were higher in 1985 and 1987 than in 1986, the number of eggs laid in the outlet was approximately 2 times higher in 1985 and 1987 than in 1986; the number laid in the lake in 1985 was likewise twice as high as in 1986. In 1987 we estimated somewhat fewer reproductive females in Emerald Lake than in 1985, with slightly lower egg production per female; accordingly, they deposited only 1.5 times as many eggs as the 1986 females.

Given the fecundity of lake females in 1985, 1986 and 1987 (300 eggs/female, 150 eggs/female and 280 eggs/female) and the number of eggs per redd (45 eggs/nest in 1985, the only year for which we have data), we calculated that each lake female constructed from 3 to 6 nests. Although the number of eggs laid in the Emerald Lake system in 1985 was approximately twice as high as in 1986, the number of YOY produced from the 1986 eggs was over 3 times higher. In contrast, spawners in 1987 laid slightly fewer eggs than in 1985, but the number of YOY appearing in 1988 (from 1987 eggs) was greater than the combined output of both earlier years. Only 0.07% of the eggs produced in 1985, 0.5% of the eggs produced in 1986 and 0.4% of those produced in 1987 survived to become YOY the following summer. These very low survival rates can be attributed to a combination of superimposition and cannibalism at the time of spawning, and to physical disturbances (floods, interstitial ice, and drought) which killed early embryos or sac fry. Only 1 to 3% of eggs deposited in Emerald Lake and 7 to 12% of those deposited in the outlet survived to the end of the spawning period. It was apparent that there was insufficient gravel for spawning and intense competition for nest sites. The gravel in spawning sites was constantly worked over by spawning females, and later spawners probably destroyed the eggs of early spawners (Hayes 1987). Exposed eggs were readily consumed by attending males in Emerald Lake, and uncovered eggs were observed in the outlet. The number of nests and embryos present in the outlet at the end of the spawning season was similar in 1985, 1986 and 1987 (54, 56 and 57 nests, 2800, 2500 and 3600 eggs), despite very different numbers of eggs deposited. This indicates that the availability of spawning sites places severe constraints on the numbers of eggs remaining at the end of the spawning season.

Fertilization of eggs approached 100% and most eggs deposited in the outlet stream were viable. If eggs were undisturbed, survival to hatching was often very high, approaching 90% in 1985-86 (Witzel and MacCrimmon 1983). A large February flood caused by an avalanche severely scoured the outlet stream in 1986. Some embryos and sac fry were killed outright, and others were adversely affected by fine sand and debris deposited by flood waters. Despite high initial hatching success, survival in 1985-86 had dropped to 2% of the original embryo number by the end of emergence (i.e, a loss of 98% of the hatched embryos). In 1986-87, on the other hand, survival from the end of the spawning season to hatching was only 13% due to freezing of interstitial gravels. Survival subsequent to hatching was better than the year before, however, with a further loss of only 54% of the hatched embryos. In 1987-1988, survival to hatching (41%) was intermediate to the other years. The likely cause of mortality was temporary cessation of stream flow over the buried eggs. As in 1987, the sac fry suffered a moderate loss from hatching to the end of emergence (66%). In general, then, it appears that physical disturbances, such as floods, droughts, and interstitial ice formation, are not uncommon and are a major cause of mortality for eggs and sac fry. Even in the absence of catastrophic events, however, it appears that fewer than 50% of the fish that hatch survive through emergence. During most of the years for which we have data (1984-1988), the pH of Emerald outlet dropped to around 5.6-5.8 during the time that some fish were attempting to emerge from the gravel (Chapter III in this report). Since pHs in this range have been shown to affect the survival of pre-emergent sac fry in the laboratory (Menendez 1976), we cannot dismiss the possibility that acidification is contributing to mortality at emergence.

Eggs hatched from January to April in 1986, from April to June in 1987 and from January through May in 1988. Eggs hatched earlier in 1986 and 1988 than in 1987 because they were laid earlier when water temperatures were higher. Emergence began in April in 1986, but was extremely protracted due to variability in hatching time. Some sac fry were still in the gravel on 15 July 1986. Emergence of fry in 1987 did not begin until early July due to late hatching, despite a relatively early snowmelt and rising water temperatures. Hatching of most embryos was again late in 1988, so emergence occurred primarily in June and July.

Recently emerged brook trout in Emerald Lake stay at the periphery in shallow water. As they grow larger, they begin to move away from shore and further from the bottom. In the outlet stream, emerging brook trout fry disperse along the channel or drop into the adjoining pond. YOY remaining in the stream stay in shallow, low velocity areas at first, but move into deeper, faster water as they grow. Fry entering the pond disperse along the shore in shallow water, much as they do in the lake. As they grow, they also tend to move into deeper water offshore. It seems likely that these changes in microhabitat choice with age reduce cannibalism, which still occurs despite the fact that YOY are spatially separated from most adults. Larger fry are faster swimmers than newly emerged fry, so they presumably can exploit food resources over a larger area without increasing their risk of predation. It is possible that the shallow habitat of early Emerald Lake fry also exposes them to lower pHs than older fish, because the acidified waters from snowmelt tend to flow over the surface of the lake.

The diets of brook trout in Emerald Lake and its outlet stream indicate that brook trout are opportunistic feeders whose diets are largely determined by prey availability (Power 1980, Allan 1981). Trout in Emerald Lake ate primarily chironomid pupae and larvae, cladocerans, and terrestrial insects in the summer and autumn, and primarily chironomid larvae and fingernail clams in the winter. Chironomids were the dominant taxa in lake benthic samples;

however, it was clear that trout feeding on zooplankton were selecting large cladocerans (Daphnia, Eurycercus) over other common zooplankton taxa, including copepods, rotifers, and small cladocerans (Melack et al. 1987). Trout in the Emerald outlet had a more diverse diet, relying on terrestrial insects and the larvae of chironomids, simuliids, trichopterans, ephemeropterans, and plecopterans in the summer and autumn. Dominant taxa in trout diets were also the dominant taxa in benthic and drift samples (Melack et al. 1987). In Emerald Lake the numbers of prey per trout stomach increased to an August or September peak, which was particularly pronounced in 1985 when trout were eating large numbers of Daphnia rosea. In contrast, numbers of prey per trout stomach declined from July to September in the Emerald outlet in both 1985 and 1986. Chironomids were more important and cladocerans less important in the diets of Emerald Lake trout in 1986 and 1987 vs. 1985. The proportional representation of simuliid and chironomid larvae in outlet trout diets was higher in 1986 than 1985, whereas terrestrial insects and ephemeropteran and plecopteran larvae showed the opposite pattern. These results parallel those reported in other studies which emphasized the importance of aquatic and terrestrial insects to lake and stream brook trout, and the importance of plankton to lake brook trout (Power 1980, McNicol et al. 1985, Grant and Noakes 1987, Allan 1981, Reimers 1958, Dawidowicz and Gliwicz 1983, Reed and Bear 1966).

There were some changes in diet with changes in trout size. Lake YOY ate primarily chironomids and cladocerans; stream YOY ate primarily chironomids in 1985 and 1986, but in 1987 cladocerans were numerically important as well. In Emerald lake intermediate size classes of trout (101-200 mm SL) ate primarily cladocerans and sometimes chironomids and terrestrial insects, whereas the largest size class (>200 mm) trout ate primarily terrestrial insects in 1985 and terrestrial insects and chironomids in 1986 and 1987. In both the lake and stream the relative representation of terrestrial insects in the diet increased with increasing fish size (see also Allan 1981). Simuliid larvae dominated the diets of stream fish >50 mm SL in 1986, while the most abundant items in the diets of trout >50 mm SL ranged from simuliid larvae (51-100 mm SL) to terrestrial insects (150-200 mm SL) in 1985.

In summary, lakes and streams in the Marble Fork basin contain dense, reproducing brook trout populations characterized by slow growth rates (particularly after age 3 years), small adult body sizes, and long-lived individuals. Low growth rate and small body size likely result from crowding relative to the food supply, which in turn results from high reproductive rate and low adult mortality. Low temperatures during much of the year undoubtedly reduce growth rates as well, but there is evidence that growth and ultimate size can be significantly greater in similar lakes with smaller brook trout densities (Hall 1988). The life histories of these populations are similar to those in many other systems, particularly lakes and streams found in northern or alpine areas. Spawning occurs in October and November, and eggs begin hatching from January to April, depending on the year. YOY emerge from the gravel between April and July. YOY grow rapidly during their first few months, but size at the end of the summer is often small owing to the short growing season. Male brook trout first become reproductively mature at age 1+ and females at age 2+. Most individuals are reproductively mature by their third year and females probably spawn at least three times during their life spans. After reproductive maturity these brook trout (especially the females) grow very little, and lake populations are dominated by fish 3 to 6 years old. Some individuals live for more than 10 years. The population sizes of trout 1+ or older stay relatively constant from year to year, and recruitment appears to compensate for the mortality of older year classes. In contrast, abundance of YOY varies greatly from year to year. The amount of usable spawning gravel is severely limited relative to the number of eggs produced each year, so the number of viable embryos present at the end of each spawning period is relatively constant. Excess eggs are destroyed by superimposition of nests. The actual strength of year classes recruited from this steady output is determined by large interannual variation in the intensity of natural catastrophes. Over the study period a variety of natural disturbances, such as floods, droughts, and interstitial ice formation, caused high mortality of early embryos or sac fry.

The diets of lake brook trout are dominated by chironomid larvae, cladocerans, and terrestrial insects, whereas the diets of stream fish are composed of terrestrial insects and a variety of aquatic insects, including simuliid, chironomid, trichopteran, ephemeropteran, and plecopteran larvae. Numbers of prey items per trout stomach tend to peak in late summer in Emerald Lake, and to decline throughout the summer in the Emerald outlet stream. There were some year to year changes in the diets of trout of different sizes. The contribution of terrestrial insects to trout diets tended to increase with increasing trout size.

Based on the literature we expect that population sizes will decrease and that the condition, size structure, and individual growth rates of fish will change should cultural acidification increase in this area. Because brook trout populations are currently dense, because condition factors are typical, because the growth of YOY is rapid, and because individual trout live a long time it is unlikely that episodic acidification is currently having any long-term impact on brook trout populations in this area. Most of the features which characterize these populations, including slow growth after the second year and the dominance of old, small individuals, can be attributed to low temperatures, short growing seasons, and crowding, as discussed above.

Of particular interest is the effect of acidification on trout recruitment. Natural egg and sac fry mortality is currently high and numbers of YOY are often low. It is apparent that the numbers of eggs present at the end of the spawning season are largely determined by the availability of suitable spawning habitat, and that many deposited eggs are lost owing to superimposition. High and variable mortality of eggs and sac fry after the spawning season are largely due to natural disturbances, such as floods, drought, or interstitial ice formation. Although we attributed low YOY recruitment in 1986 to the effects of a flood caused by an avalanche, low numbers of YOY were recorded in all lakes in the Marble Fork watershed. Although data are lacking it is unlikely that all of these lakes experienced avalanches. It would appear, then, that some factor operating over the whole basin resulted in low recruitment of YOY in 1986. Snowmelt was much later in 1986 than in 1985 or 1987, and early summer discharges were high. It is possible that this delay in warming caused additional mortality of fry (Donald and Alger 1986). On the other hand, pH depressions were recorded during snowmelt in Emerald Lake in 1986 (and to a lesser extent in 1984, 1985, 1987 and 1988). Subsurface pH in peripheral areas of Emerald Lake fell as low as 5.51 during snowmelt in late May-early June 1986 (M. Williams, unpublished), which would have coincided with emergence of fry. pH values were <5.7 from May 25 to June 10, and <6.0 from May 18 to July 2. Trojnar (1977) found that brook trout fry from eggs acclimated to pH 8.1 showed 25% mortality when exposed to pH 5.7, and 33% mortality when exposed to pH 5.0. Control populations at pH 8.1 only showed 4% mortality. Menendez (1976) reported that brook trout alevins (sac fry) exposed to pH 5.6 and 6.1 for 90 days had mortalities of approximately 50%. Alevins exposed to pH 7.0 had 25% mortality over the same time period. Working with the closely-related lake trout, Salvelinus namaycush, Gunn and Keller (1984) found that sac fry exposed to pHs 4.5 to 5.0 for 5 days in a lake showed 18% mortality, but less severe pH depressions had little effect on fry mortality. More data are needed to evaluate the effects of these short-term pH depressions on the survivorship of early brook trout stages. Because different strains of brook trout show different susceptibilities to reduced pH (Robinson et al. 1976, Swarts et al. 1978), it will be necessary to determine the sensitivity of the brook trout strain in Emerald Lake to acidic inputs. There is a distinct possibility that pH depressions in spring 1986 may have contributed to the mortality of brook trout YOY in that year. pH depressions of this magnitude were not encountered in spring 1985, when YOY recruitment was much higher, but data from 1987 suggest that emergence may never exceed 50% of viable sac fry.

Additional mortality of early stages owing to acidification could result in recruitment failure. Recruitment failure could also result from delayed maturity and egg hatching, decreased fecundity and fertility, and delayed or inhibited spawning resulting from increased acidic inputs. As yet, there is little evidence for any of the above phenomena. Decreased fecundity in 1986 vs. 1985 and 1987 was associated with overall depressions in condition factor indicating that reduced fecundity resulted from factors operating throughout the summer. The most likely explanation for reduced fecundity in 1986 was the late snowmelt and consequent short feeding period before spawning. Time for accumulating energy reserves was presumably too short for maximum egg production.

Cultural acidification could also affect trout populations indirectly by altering their food supplies. Prey of aquatic origin provided approximately 60 to 70% of prey items by number for brook trout in Emerald Lake, and 70 to 90% of the diets of Emerald outlet trout. Comparisons with hatchery-reared fish and fish in sparsely-populated lakes at high elevations (T. Jenkins, personal observations) indicate that these brook trout are growing at a fraction of their potential rate. For example, a fish caught by gill net in Pear Lake was 350 mm long, or nearly twice the size of other fish caught or observed underwater. It contained several smaller trout, suggesting that a better diet can produce faster growth even in these severe physical conditions. Because food is so obviously limited, we can expect that trout growth and diet would be highly sensitive to acid-induced changes in the aquatic community.

For example, our ARB-supported limnological experiments have shown that the zooplankton species Daphnia rosea is highly sensitive to acidic inputs, nearly disappearing from the system at pH's as high as 5.5 (Melack et al. 1987, Chapter VI in this report). Cultural acidification would probably eliminate this species from Emerald Lake with important repercussions for trout populations, because Daphnia rosea is the dominant zooplankton species found in trout diets in Emerald Lake. Trout sensitivity to shifts in their aquatic prey may be particularly pronounced in the winter when lake fish are largely restricted to food from aquatic sources.

In the summer, larvae of the Pacific tree frog, Hyla regilla, are present in a number of ponds in the Emerald Lake area. Eggs are laid in these ponds shortly after snow melt and the larvae develop quickly, metamorphosing by September. Population sizes, developmental and growth rates, and the timing of metamorphosis are variable among these ponds, probably due to differences in temperature, exposure, and chemistry. The occurrence and abundance of larvae in ponds appeared unrelated to pond size, degree of permanence, elevation, or pH. Catastrophic events, such as pond drying or early freezing, decimated tadpole populations in some ponds. The incidence of physical abnormalities was very low.

Because larval amphibian habitats are small and poorly-buffered, water quality changes following snow melt or rains may occur. Larval amphibian habitats are used only in the spring and summer, when episodic surface-water acidification has been observed in Emerald Lake. The literature indicates that larval amphibians show sensitive responses to acidic inputs, including changes in population size, reproduction, and growth and development. Should cultural acidification occur in this area, we expect larval amphibians to display delayed or inhibited metamorphosis, reduced growth and developmental rates, increased mortality, increased incidence of abnormalities and lower recruitment owing to difficulties in egg hatching. The result of some of these responses should be the reduction or elimination of amphibian populations from some ponds. At present, there is little evidence for any of these demographic indicators of acid stress. Over the study period amphibian populations were not lost from ponds, and ponds containing high larval densities one year had high larval densities in subsequent years. Growth and development was rapid, the incidence of abnormalities was very low, and drastic increases in mortality could usually be attributed to physical disturbances, such as pond drying or freezing. The limited data on hylid frogs show that they are very tolerant of low pH, only exhibiting high mortality when pH is reduced to approximately 4.0 (Gosner and Black 1957). Ponds in the Marble Fork basin did not have pHs <5.3, and there was no relationship between the occurrence of tadpoles and pond pH.

Our data indicate that trout and amphibian populations in the Emerald Lake area are similar to those in other parts of the Sierra Nevada. It should be emphasized, however, that the population characteristics that we are monitoring need to be measured for a number of years so that we can determine natural variability in this system. It is essential that ecological data be collected continuously over a number of years in order to separate the effects of anthropogenic disturbance from natural variation. Because the population characteristics of fish and amphibians vary greatly from year-to-year, it is necessary to collect long-term data sets to examine the extent of this temporal variation. Furthermore, many ecological changes may occur slowly so it is necessary to collect data for long time periods so that general trends can be evaluated. Because natural variation may obscure these general trends, long-term data sets are needed to discern patterns given the "noise" generated by natural changes.

Our data not only indicate that our study sites are representative of other aquatic habitats in the High Sierra, but that they are currently not greatly affected by cultural acidification. Surface-water acidification in Emerald Lake has occurred during snowmelt and after an intense rainstorm, however, indicating that ephemeral chemical changes can occur as a result of acid inputs (Melack et al. 1987). Although the data are not conclusive, it is possible that poor YOY recruitment in 1986 was associated with increased mortality of early stages owing to disturbances related to avalanches, delayed snow melt and high run-off, and pH depressions. Because our study systems are poorly-buffered they will likely change in chemical and, consequently, biological characteristics should increased cultural acidification occur. As an important part of the Integrated Watershed Study, our studies of fish and amphibians will contribute to use of the Emerald Lake system as a potent indicator of environmental stress.

Table IX-1. Physical characteristics and representative pH of surveyed lakes.

Lake	Altitude (meters)	Max. Depth (meters)	Area (hectares)	Basin Area (hectares)	pH
Emerald	2800	10.5	2.72	120	6.3
Heather	2804	6.5	2.07	57	6.4
Pear	2877	27.0	8.0	136	6.4
Aster	2743	11.0	1.83	135	6.5

'able IX-2. Census data for Emerald Lake and other waters of the upper Marble Fork, Kaweah River: 1985-1987. 0+= young-of-year, A= adult. T= total number of different individuals handled during a field season. J-S (July- Sept) indicates repeated trapping during the summer for mark-recapture estimates. "Best Estimates" are single values (or means when several comparable estimates are available), or the highest count of 2 or more direct counts.

System	Age	Date	Est(95% CI)	Method	Best Estimate (95% CI)
Emerald Lake	0+	8-85	428	Count	428
		8-85	351		
		9-85	266		
	A	9-85	1263(677-2256)	Mark-recap	
		10-85	908(515-1557)		
		10-85	1225(578-2357)		1132(907-1357)
	0+	8-86	67	Count	67
		8-86	64		
		9-86	66		
		10-86	7		
		10-86	25		
	A	9-86	928(461-1740)	Mark-recap	
		9-86	812(330-1624)		
		10-86	1814(737-3627)		
		10-86	1123(497-2213)		1169(720-1618)
	0+	6-87	79	Count	
		7-87	166		
		8-87	323		323
			126		
			251		
		9-87	26		
		10-87	21		
	A	9-87	984(400-1968)	Mark-recap	
		9-87	688(325-1324)		
		9-87	837(395-1610)		
		9-87	1566(839-2796)		
		9-87	1107(522-2130)		1036(736-1336)
Emerald Outlet	0+	8-85	107	Count	
		8-85	198		198
	A	7-85	58(44-72)	Depletion	58(44-72)
		8-85	115(56-173)	Mark-recap	
		9-85	155(107-281)		
		9-85	55(54-56)		97(49--145)
		T	113	Count	113

Table IX-2. (Continued) Census data for Emerald Lake and other waters of the upper Marble Fork, Kaweah River: 1985-1987.

System	Age	Date	Est(95% CI)	Method	Best Estimate (95% CI)
Emerald Outlet	0+	9-86	15	Count	
		9-86	26		26
		9-86	21		
		10-86	14		
	A	7-86	63(37-88)	Depletion	
		8-86	53(38-69)		
		9-86	31(27-35)		49(30-68)
		8-86	203(100-305)	Mark-recap	
		9-86	240(120-360)		222(185-259)
		T	104	Count	104
	0+	6-87	0	Count	
		7-87	46		
		7-87	37		
		8-87	53		
		8-87	66		
		9-87	101		101
		9-87	65		
	A	7-87	77(65-89)	Depletion	
		9-87	56(52-61)		67(46-88)
		9-87	190(131-248)	Mark-recap	190(131-248)
		T	137	Count	137
Pond 1	0+	8-86	38	Count	38
		10-86	3		
			12		
			19		
			8		
	A	J-S	159(122-226)	Mark-recap	159(122-226)
	0+	6-87	3	Count	
		7-87	45		
		7-87	50		
		8-87	29		
		8-87	51		
		8-87	44		
		9-87	27		
		9-87	36		
		9-87	51		51
	A	J-S	238(192-312)	Mark-recap	238(192-312)

Table IX-2. (Continued) Census data for Emerald Lake and other waters of the upper Marble Fork, Kaweah River: 1985-1987.

System	Age	Date	Est(95% CI)	Method	Best estimate (95% CI)
Pond 2	0+	10-86	3	Count	3
	A	9-86	217(120-379)	Mark-recap	217(120-379)
	0+	6-87	0	Count	
		7-87	12		12
		8-87	3		
		8-87	1		
		9-87	1		
	A	9-87	320(237-403)	Mark-recap	320(237-403)
Mid-outlet	A	7-85	34(22-47)	Depletion	34(22-47)
		8-85	135(49-266)	Mark-recap	135(49-266)
Aster Inlet	A	7-85	27(21-33)	Depletion	27(21-33)
		8-85	99(40-198)	Mark-recap	99(40-198)
Aster Lake	0+	9-85	262	Count	262
	A	9-85	764(433-1309)	Mark-recap	
		10-85	1599(577-3145)		1182(347-2017)
	0+	10-86	29	Count	29
	0+	9-87	130	Count	130
Aster Outlet	A	7-85	27(23-30)	Depletion	27(23-30)
		8-85	72(29-144)	Mark-recap	72(29-144)
Heather Lake	0+	9-85	242	Count	242
	A	9-85	828	Mark-recap	828
	0+	10-86	10	Count	10
	0+	9-87	100	Count	100
Heather Outlet	A	7-85	9	Count	9
	A	9-86	9	Count	9

Table IX-2. (Continued) Census data for Emerald Lake and other waters of the upper Marble Fork, Kaweah River: 1985-1987.

System	Age	Date	Est(95% CI)	Method	Best Estimate (95% CI)
Heather Outlet	A	7-87	15	Count	15
Pear Lake	0+	9-85	932	Count	932
	A	9-85	663	Mark-recap	663
	0+	9-86	76	Count	76
	0+	9-87	571	Count	571
Pear Outlet	A	7-85	7(6-9)	Depletion	7(6-9)
		8-85	32(10-56)	Mark-recap	32(10-56)

Table IX-3. Estimates of brook trout biomass in the study waters. based on Petersen mark-recapture estimates and average weight of samples (Heather outlet population based on direct count). Area of streams is based on a width of 1 meter except for Heather Outlet, with a width of 0.25 m, and Emerald outlet, which was measured directly. EL=Emerald Lake; AL=Aster Lake; HL=Heather Lake; PL=Pear Lake; P1=Pond 1; P2=Pond 2; EO=Emerald Outlet; AI=Aster Inlet; AO=Aster Outlet; HO=Heather Outlet; PO=Pear Outlet.

Water(year)	Mean Weight (g)	Biomass (Kg)	Area (Ha)	Density (Kg/Ha)
EL(85)	81.8	92.6	2.85	32.5
EL(86)	79.4	92.8	2.85	32.6
EL(87)	78.8	81.6	2.85	28.6
AL(85)	69.3	81.9	1.83	44.8
HL(85)	86.1	71.3	2.07	34.4
PL(85)	100.9	66.9	6.80	9.8
P1(86)	42.1	6.7	0.113	59.3
P1(87)	42.7	10.2	0.113	90.3
P2(86)	18.1	3.9	0.071	54.9
P2(87)	26.5	8.5	0.071	119.7
EO(85)	40.6	7.6	0.021	361.9
EO(86)	44.6	9.9	0.021	471.5
EO(87)	40.7	7.7	0.021	368.2
AI(85)	43.6	4.3	0.01	431.6
AO(85)	63.6	4.6	0.01	457.9
HO(85)	104.5	0.9	.0025	376.2
PO(85)	71.1	2.3	0.01	227.5

Table IX-4. Comparison of size-age statistics for the Emerald Lake system brook trout. Included are the outlet and both outlet ponds. Ages are from otolith readings, and are rounded to the nearest year. Emerald Lake, Emerald Outlet and Pond 1 data are from 1985 and 1986. Pond 2 ages are from 1986 collections only.

Habitat	Standard Length (mm)	Age(years)									
		1+	2+	3+	4+	5+	6+	7+	8+	9+	10+
EL	Mean	98	139	168	172	183	183	189	179	188	190
	SE	19	11	6	4	4	3	9	1	7	-
	N	3	5	8	18	25	21	9	2	2	1
EO	Mean	86	110	136	142	152	177	181			
	SE	4	8	25	7	10	22	6			
	N	8	5	3	3	2	2	3			
P1	Mean	95	119	128	149	175	175				
	SE	5	9	9	-	-	-				
	N	3	3	3	1	1	1				
P2	Mean	84	106	133			171	184			
	SE	2	-	-			4	-			
	N	2	1	1			2	1			

Table IX-5. Whole body lipid content of brook trout from selected lakes in the upper Marble Fork, Kaweah River.

Habitat	Date	Sample size	Lipid content (% dry weight)	
			Mean	SE
Emerald L.	10-86	10	10.5	.91
	1-87	3	5.8	1.01
	2-87	7	6.1	.83
	3-87	4	6.6	1.40
	4-87	2	8.3	1.88
	5-87	10	5.9	.76
Aster L.	10-86	10	11.6	1.63
Heather L.	10-86	10	10.0	1.24
Pear L.	10-86	10	7.5	1.81

Table IX-6. Characteristics of nests and their surroundings in Emerald Outlet, 1985-1987. Velocity is speed of water approximately 1 cm above the gravel surface. All depths are in centimeters. N = sample size.

Year	Statistic	Water Depth over Gravel	Minimum Burial depth	Maximum Burial depth	Velocity (cm/sec)
1985					
	Mean	11.8	4.8	11.0	10.2
	SE	1.0	0.2	0.5	0.7
	N	54	54	19	54
1986					
	Mean	13.0	3.8	7.1	6.7
	SE	0.8	0.2	0.4	0.2
	N	56	56	26	56
1987					
	Mean	13.1	4.1	8.7	5.2
	SE	0.8	0.2	0.6	1.2
	N	57	57	22	57

Table IX-7. Summary of reproductive success of Emerald basin brook trout, including fish from Emerald Lake, Emerald outlet, Pond 1, and Pond 2 (in 1985). Estimates are based on fish numbers, fish sizes, egg counts in pre-reproductive females, and live embryo counts at intervals through development periods. EO+P1+EL(+P2) refers to fish spawning in Emerald outlet, including fish from the ponds and Emerald Lake. We have seen no indication that age 0 fish return to the lake from the stream, so all fry in this count were in the outlet or Pond 1.

		Spawning Oct-Dec		Development Oct-June	Fry stage June-
Year	Habitat	Eggs Expended	Eggs Surviving	Embryos Hatching	0+ fish Observed
84-85	EL	-	-	-	428
	EO+P1+EL	-	-	-	>>198
	P2	-	-	-	-
	TOTAL	-	-	-	>626
85-86	EL	145 000	2 200	-	67
	EO+P1+EL+P2	40 000	2 800	2 500	64
	P2	16 000	-	-	3
	TOTAL	201 000	-	-	134
86-87	EL	75 000	2 200	-	323
	EO+P1+EL	20 000	2 500	325	152
	P2	8 000	-	-	12
	TOTAL	103 000	-	-	487
87-88	EL	120 000	2 200	-	295
	EO+P1+EL	53 000	3 600	1 400	489 -
	P2	23 000	-	-	-
	TOTAL	196 000	-	-	784 -

Table IX-8. Percent of pre-hatching embryos surviving in "6-pack" modules at different intervals after fertilization in Emerald Outlet during the winters of 1985-86, 1986-87 and 1987-88.

	1985-86			1986-87			1987-88		
Days	n	Mean %	SE	n	Mean %	SE	n	Mean %	SE
0	9	98	1	12	99	0.4	12	96	1
10	1	100	-						
20	3	96	4						
30	5	83	7	1	0	-			
40	1	0	-	2	94	6			
50	3	100	0	3	93	7	5	57	16
60	5	88	5	4	75	25			
70	1	25	-	4	70	24	5	71	17
80	5	89	5	4	0	0	3	66	14
90	3	96	4	4	20	20	1	94	-
100				4	15	15	7	45	18
110				4	8	5	3	79	8
120	3	90	10	4	25	25	3	44	6
130				4	13	13			
140				4	5	5	4	24	19
150	2	75	4	3	33	33			
160				3	13	13			
170				2	0	0	1	67	-
180	2	83	3	2	0	0			

Table IX-9. Food of brook trout in the Emerald Lake basin during the winters of 1986 and 1987. Values are percent by number of pooled stomach contents.

	EL					EO
Date	1-86	2-86	5-86	1-87	2-87	1-86
Sample size	2	6	4	3	3	1
Chironomid larvae	26	90	84	14	57	12
Pisidium	74	6	8	27	37	
Cladocera				44		
Copepoda		2		16	5	
Plecoptera			1			12
Trichoptera					1	12
Simuliid larvae						38
Misc. Aquatic		2				
Terrestrial			7			25

Table IX-10. Effect of fish size on taxonomic composition of brook trout diets. Emerald Lake, 1985. Diet is expressed as percent contribution of different prey groups, by number.

	Standard Length (mm)				
Prey taxon	0-50	51-100	101-150	151-200	201-250
Chironomid larvae	23	2	1	1	0
Chironomid pupae	12	15	1	3	1
Ephemeroptera	0	0	0	0	0
Trichoptera	0	0	0	0	1
Cladocera	49	78	98	82	9
Copepoda	6	0	0	0	0
Arachnida	1	3	0	0	0
Pisidium	0	0	0	0	0
Misc. aquatic	0	0	0	0	8
Terrestrial	9	2	0	14	81
Sample size	10	5	12	73	5
Mean number/stomach	57	344	1515	490	137

Table IX-11. Effect of fish size on taxonomic composition of brook trout diets. Emerald Lake, 1986. Diet is expressed as percent contribution of different prey groups, by number.

	Standard Length (mm)				
Prey taxon	0-50	51-100	101-150	151-200	201-250
Chironomid larvae	27	57	7	26	24
Chironomid pupae	11	10	11	17	39
Ephemeroptera	0	0	0	2	1
Trichoptera	0	0	0	1	1
Cladocera	38	7	71	28	3
Copepoda	1	7	0	0	0
Arachnida	1	1	0	0	0
Pisidium	0	0	4	1	9
Misc. aquatic	0	0	1	1	0
Terrestrial	22	18	6	24	23
Sample size	14	2	14	63	9
Mean number/stomach	49	23	192	218	119

Table IX-12. Effect of fish size on taxonomic composition of brook trout diets, Emerald Lake, 1987. Diet is expressed as percent contribution of different prey groups, by number.

	Standard Length (mm)				
Prey taxon	0-50	51-100	101-150	151-200	201-250
Chironomid larvae	67	4	17	7	1
Chironomid pupae	14	4	20	30	30
Ephemeroptera	0	0	0	0	0
Trichoptera	0	0	0	0	0
Cladocera	11	88	51	41	1
Copepoda	4	2	0	0	0
Arachnida	1	0	4	5	10
Pisidium	0	0	0	0	0
Misc. aquatic	0	0	0	0	0
Terrestrial	4	2	8	17	58
Sample size	11	14	12	67	3
Mean number/stomach	39	222	123	168	115

Table IX-13. Effect of fish size on taxonomic composition of brook trout diets. Emerald Outlet, 1985. Diet is expressed as percent contribution of different prey groups, by number.

Prey taxon	Standard Length (mm) 0-50	51-100	101-150	151-200	201-250
Chironomid larvae	79.3	28.7	14.6	7.4	-
Chironomid pupae	1.9	0.8	3.7	1.3	-
Simuliid larvae	7.2	42.1	14.6	13.5	-
Simuliid pupae	0	0.8	0.8	3.3	-
Ephemeroptera	0.5	2.2	4.5	8.5	-
Trichoptera	0.9	3.3	19.9	9.6	-
Plecoptera	0.5	6.0	11.4	8.7	-
Misc. aquatic	6.3	2.4	6.1	5.0	-
Terrestrial	3.4	13.7	24.4	42.7	-
Sample size	8	8	16	33	0
Mean number/stomach	26	46	15	14	-

Table IX-14. Effect of fish size on taxonomic composition of brook trout diets, Emerald outlet, 1986. Diet is expressed as percent contribution of different prey groups, by number.

Prey taxon	Standard Length (mm)				
	0-50	51-100	101-150	151-200	201-250
Chironomid larvae	58.6	20.9	16.6	10.5	-
Chironomid pupae	13.2	13.9	12.4	3.3	-
Simuliid larvae	1.4	20.9	52.7	51.0	-
Simuliid pupae	0	0	0.7	0.4	-
Ephemeroptera	1.9	2.5	0.6	0.3	-
Trichoptera	0.2	12.9	11.0	14.0	-
Plecoptera	1.6	0	0.6	0.1	-
Misc. aquatic	0.8	1.0	1.3	0.5	-
Terrestrial	8.2	19.4	4.1	19.9	-
Cladocera	14.2	8.5	0	0	-
Sample size	12	5	9	9	0
Mean number/stomach	43	40	75	102	-

Table IX-15. Effect of fish size on taxonomic composition of underyearling brook trout diets, Emerald outlet, 1987. Diet is expressed as percent contribution of different prey groups, by number.

Prey taxon	Standard Length (mm)	
	0-50	51-100
Chironomid larvae	43.1	34.3
Chironomid pupae	3.3	3.3
Simuliid larvae	2.2	0
Simuliid pupae	0	0
Ephemeroptera	1.3	0
Trichoptera	0.1	0
Plecoptera	0.5	0
Misc. aquatic	1.3	2.1
Terrestrial	1.2	3.8
Cladocera	47.1	56.5
Sample size	14	7
Mean number/stomach	78	116

Table IX-16. Effect of fish size on taxonomic composition of underyearling brook trout diets, Pond 1, 1986, 1987. Diet is expressed as percent contribution of different prey groups, by number.

	Standard Length (mm)			
	1986		1987	
Prey taxon	0-50	51-100	0-50	51-100
Chironomid larvae	32.0	19.7	75.4	30.4
Chironomid pupae	5.4	0	4.2	1.1
Ephemeroptera	0.2	0	0.1	0
Trichoptera	0.1	0	0	0.2
Cladocera	47.6	79.9	17.0	56.7
Copepoda	11.7	0	0.7	0.3
Arachnida	0.1	0.3	0.1	0.2
Pisidium	0	0	0	0
Misc. Aquatic	0.5	0	0.6	0.3
Terrestrial	2.4	0	1.9	10.9
Sample size	14	1	12	8
Mean number/stomach	60	294	73	82

Table IX-17. Characteristics of amphibian ponds surveyed in the Marble Fork drainage, 1985-1987. Pond size was determined by depth and surface area: S = < 25 m^2 and < 0.5 m deep, M = 25-300 m^2 and ≤ 1.0 m deep, L = > 300 m^2 and deeper than 1.0 m. Pond duration was categorized as either permanent or ephemeral depending on whether it retained water throughout the study period. Relative densities are indicated as no amphibians (0), L = one or less larval amphibian per m^2 and H = greater than one larval amphibian per m^2. Presence (%) of amphibian larvae is represented as the number of visits when amphibian larvae were present per total number of visits to a particular pond.

Pond	Elevation (meters)	Pond Size	Duration	Relative Density	Presence (%)
Dead Snag	2804	M	E	L	50
Pear-Emerald Ridge	2914	M	E	H	67
N Aster	2762	M	E	H	60
S Aster	2768	M	E	L	14
SW Aster (188°)	2780	M	P	H	69
W Emerald (286°)	2804	M	P	0	0
Hidden	2792	L	P	L	22
W. Emerald (274°)	2792	S	E	H	71
Tent	2786	M	E	H	65
Trail	2786	S	E	H	100
Why	3158	S	E	H	64
Upper Pear Basin	3109	L	P	L	54
Parson's	2963	L	P	0	0
E Heather (lower)	2865	S	E	0	0
E Heather (upper)	2871	M	E	H	80

Table IX-18. Comparison of pH and acid neutralizing capacity (ANC) between ponds containing amphibians (larvae present at least 50% of all visits) and ponds containing no amphibians (larvae present less than 25% of all visits). Values are means for all samples taken over the sampling period (June through September) for each year.

Year,	pH			ANC ($\mu eq\ L^{-1}$)		
Pond Type	n	mean	range	n	mean	range
1985						
Amphibians	10	5.8	5.3-6.9	--	--	--
No Amphibians	3	6.6	6.4-7.0	--	--	--
1986						
Amphibians	14	5.9	5.5-6.7	14	51	19-132
No Amphibians	8	6.2	5.9-6.5	8	51	20- 85
1987						
Amphibians	21	5.9	5.4-7.2	21	52	0-130
No Amphibians	15	6.2	5.7-6.8	15	63	20- 92
All Years						
Amphibians	45	5.9	5.3-7.2	35	50	0-132
No Amphibians	26	6.2	5.7-7.0	23	59	20- 92

Fig. IX-1. Locations of lakes, ponds and streams sampled for fish and amphibians.
X = vernal ponds surveyed for amphibians.

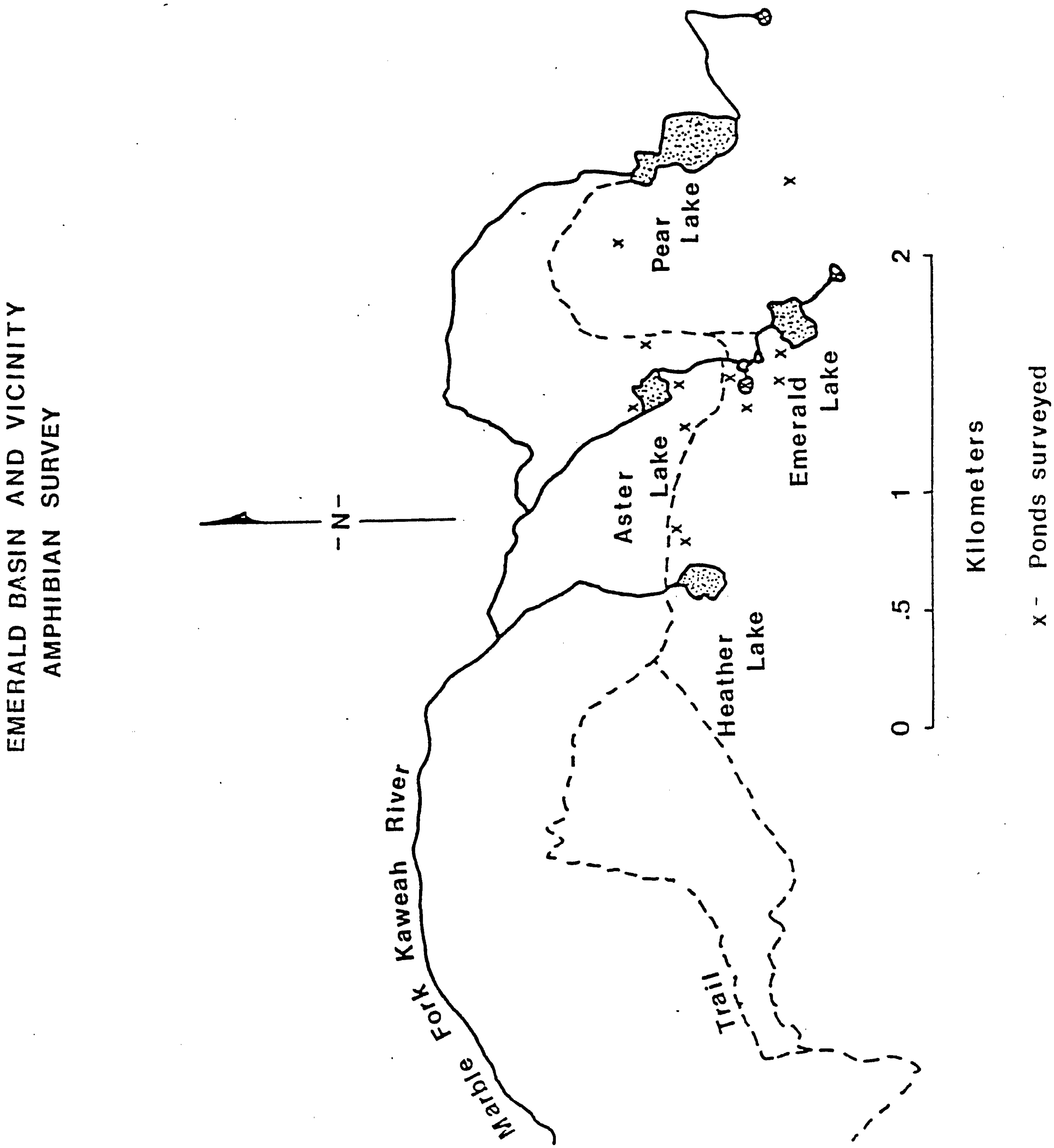


Fig. IX-2. Emerald Lake and its outlet system, including the outlet stream and Ponds 1 and 2.

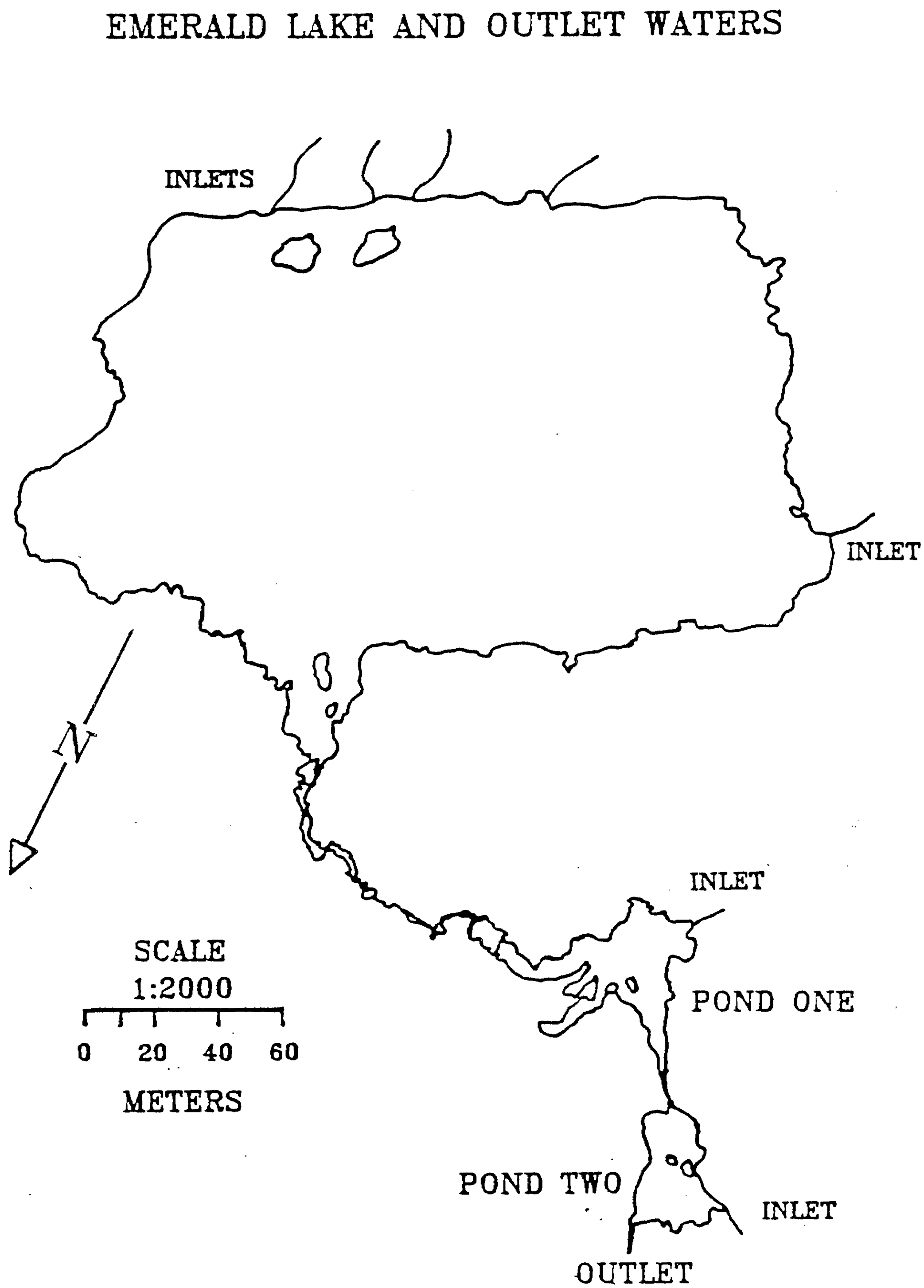


Fig. IX-3. The number of fish taken in 5-mm length classes in 4 study lakes. EL - Emerald Lake; AL - Aster Lake; HL - Heather Lake; PL - Pear Lake.

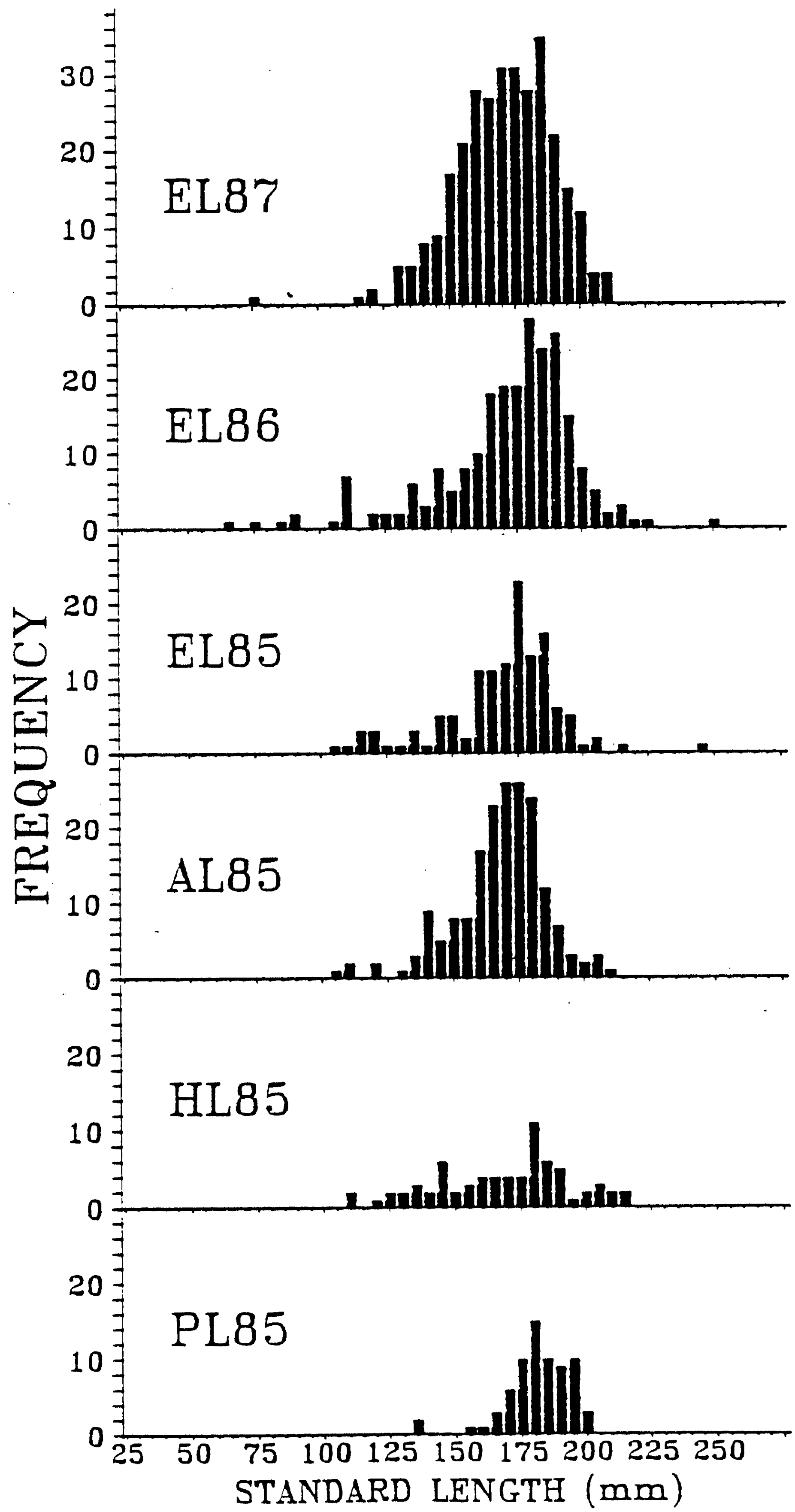


Fig. IX-4. Frequency of length classes for Emerald Lake brook trout during the summer and fall months of 1985. (Young-of-year were collected in July and August)

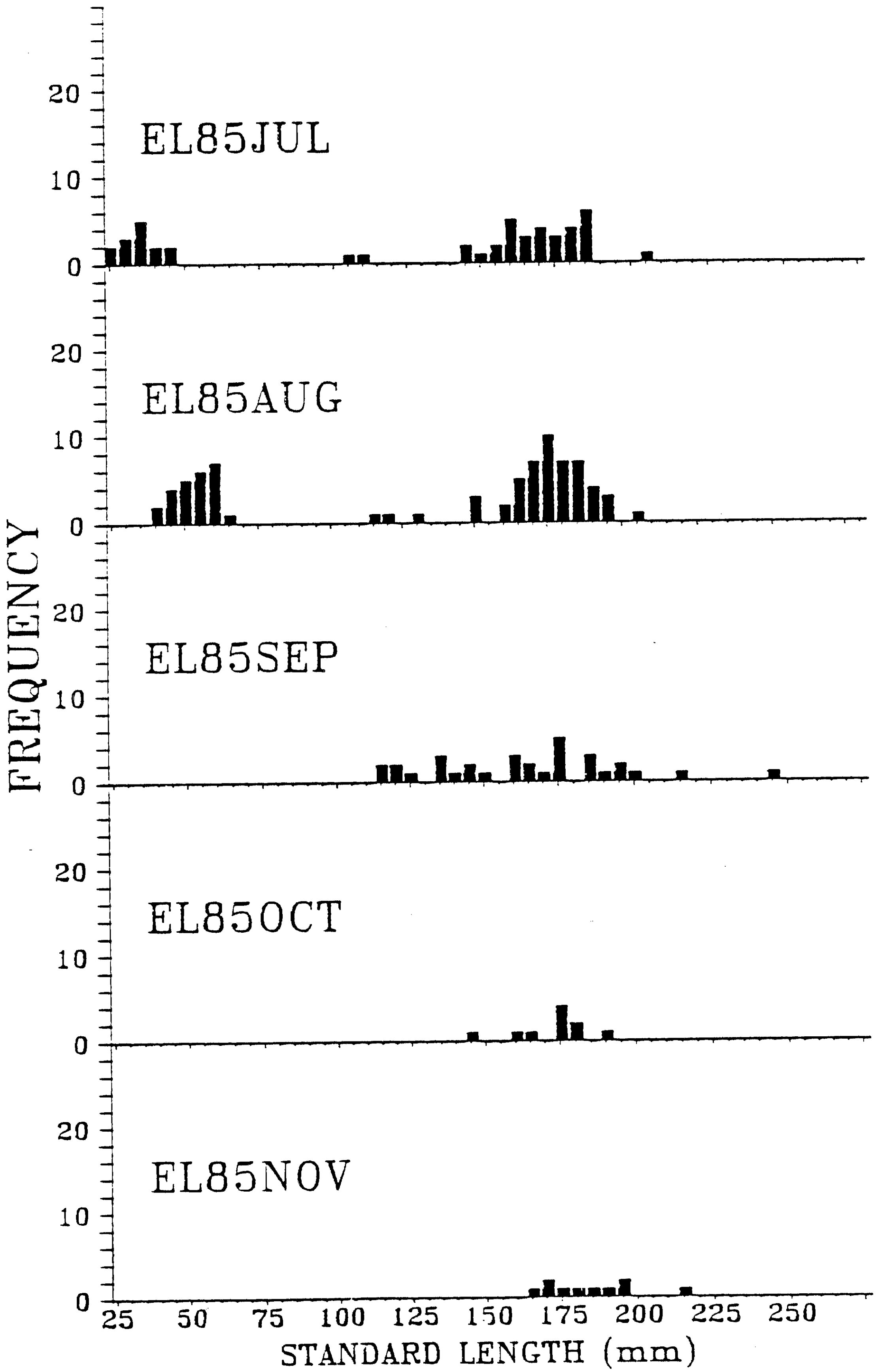


Fig. IX-5. Frequency of length classes for Emerald Lake brook trout during the summer and fall months of 1986. (Young-of-year were collected Aug-Oct.)

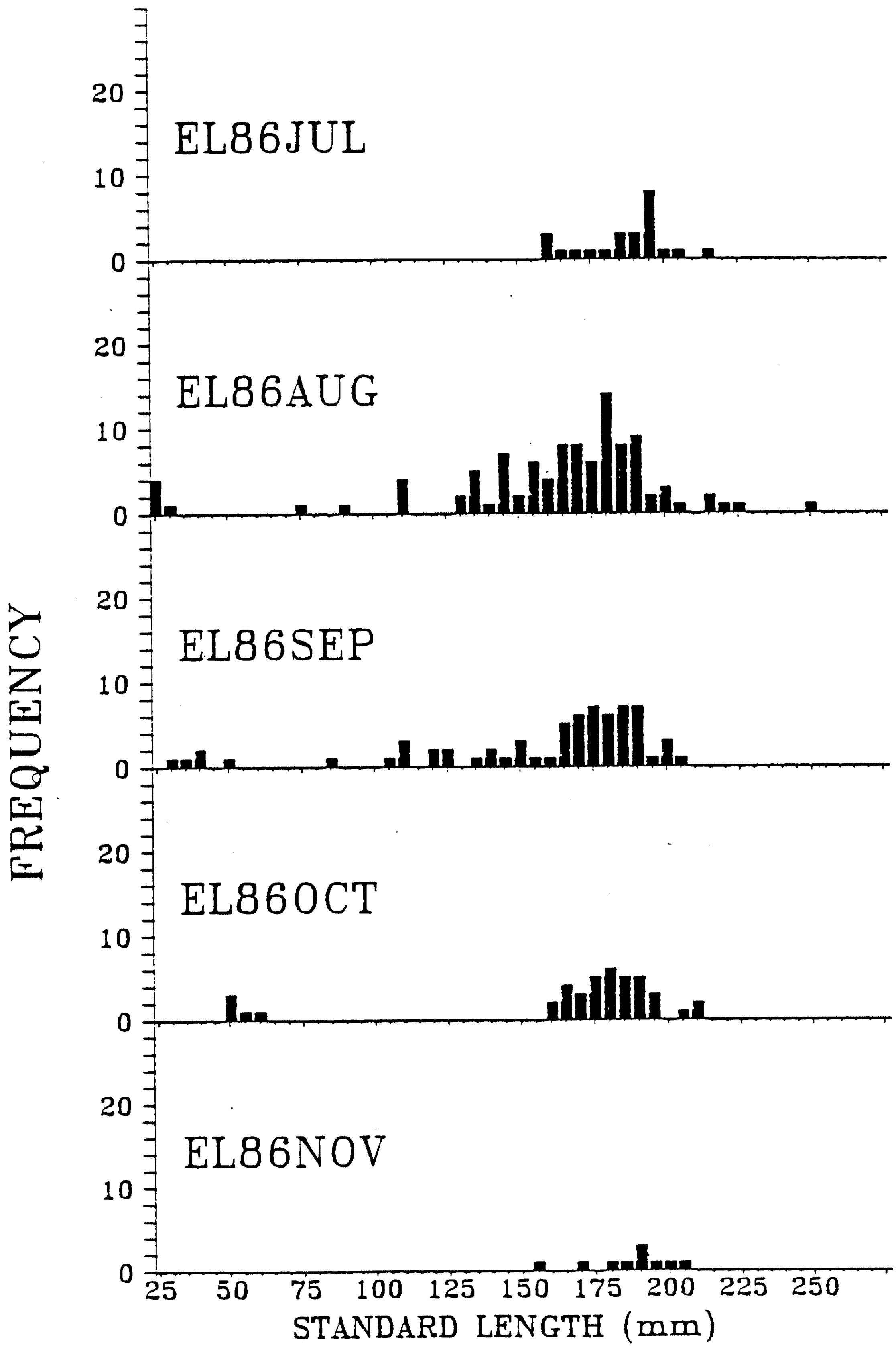


Fig 6. Frequency of length classes for Emerald Lake brook trout during the summer and fall months of 1987. (Young-of year were collected July-Oct: 4 fish in the 20-mm size class were added to the 25-mm class.)

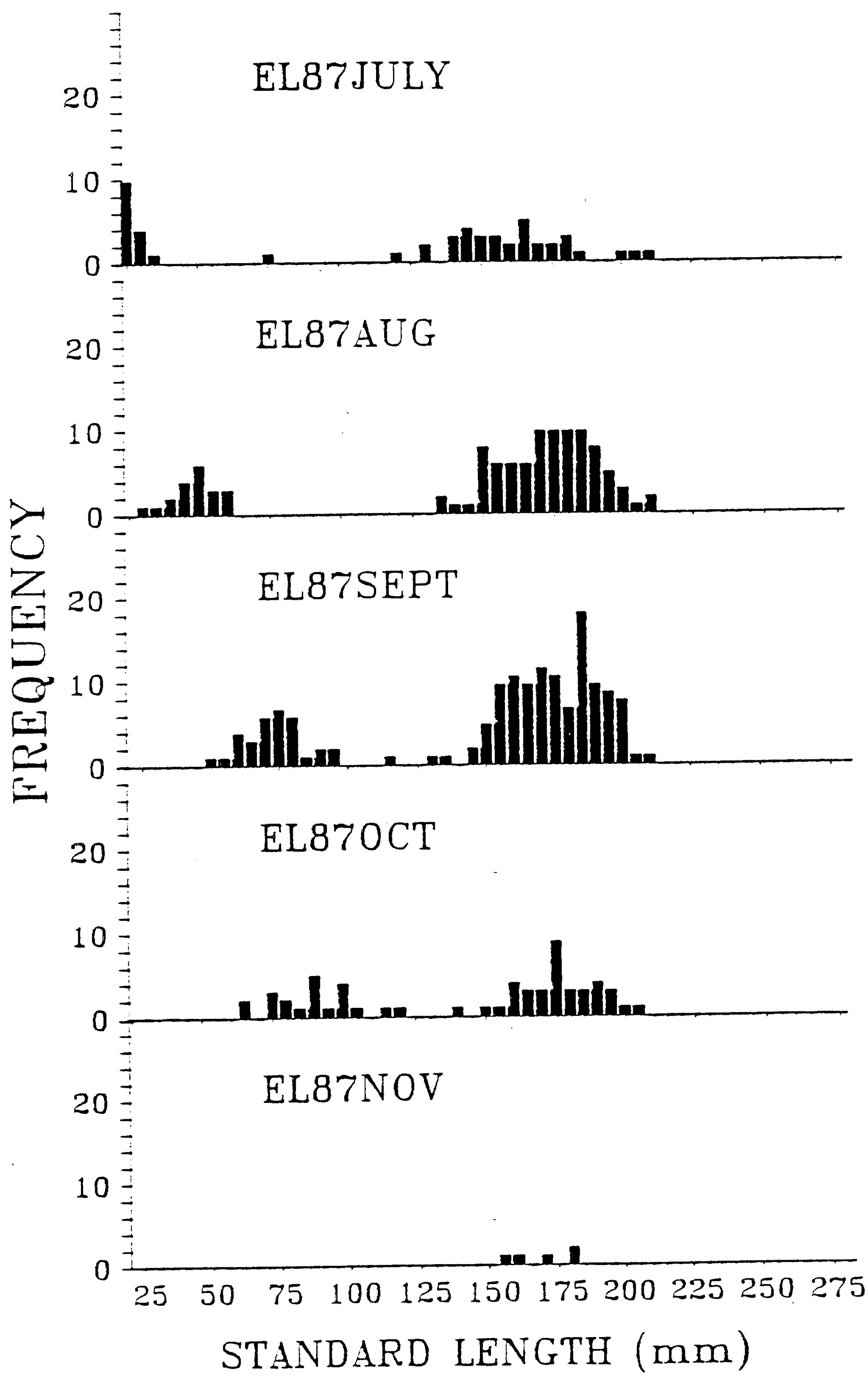


Fig. IX-7. Size distribution of juvenile and adult brook trout in the Emerald outlet (EO) and other study streams in 1985. PO - Pear outlet, HO - Heather outlet, AI and AO - Aster inlet and outlet, MO - stream from Pond 2 to Aster inlet.

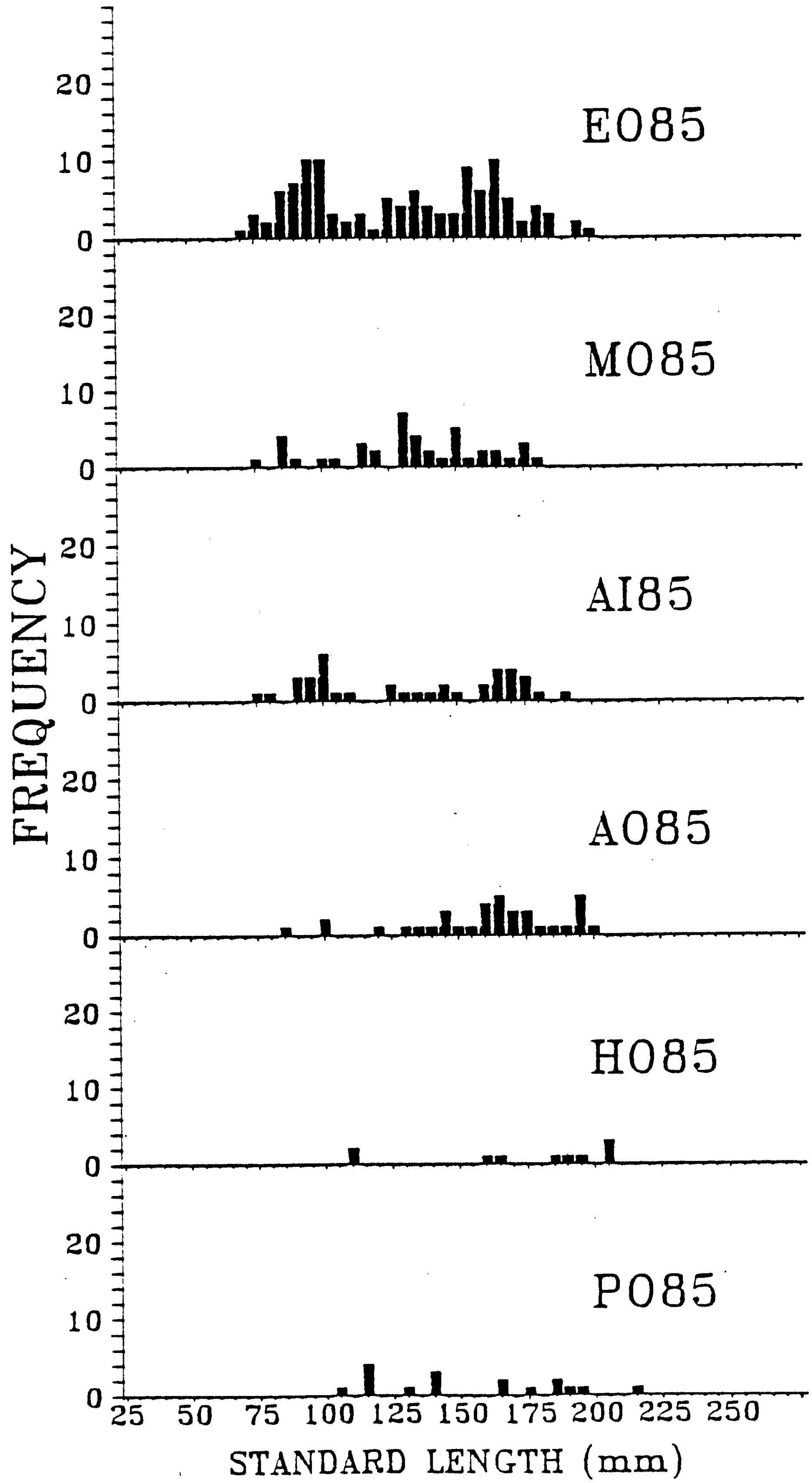


Fig. IX-8. Frequency of length classes for juvenile and adult brook trout in the Emerald outlet during the summers of 1985, 1986, and 1987.

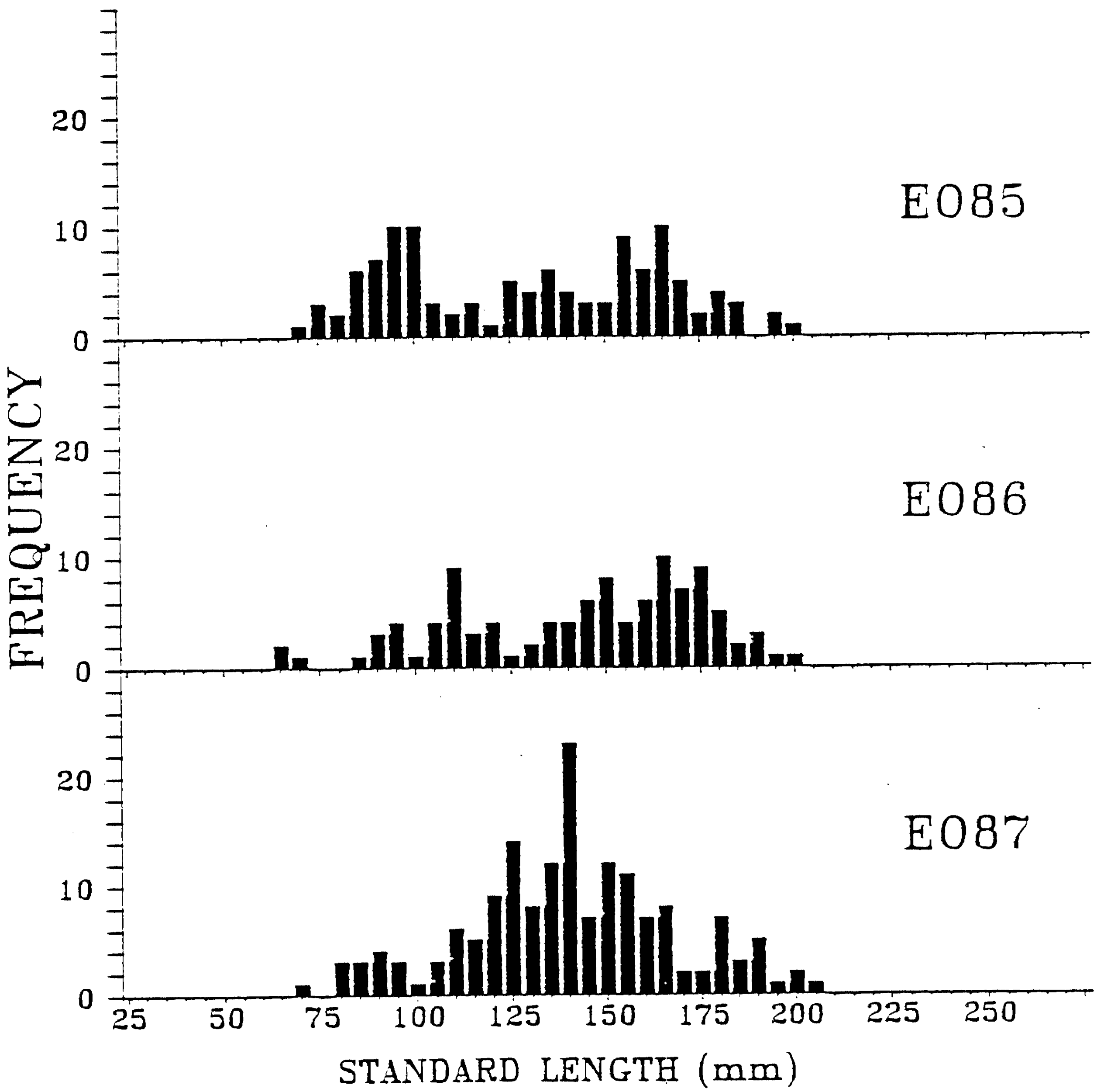


Fig. IX-9. Frequency of length classes by month in Emerald outlet, 1985-1987.

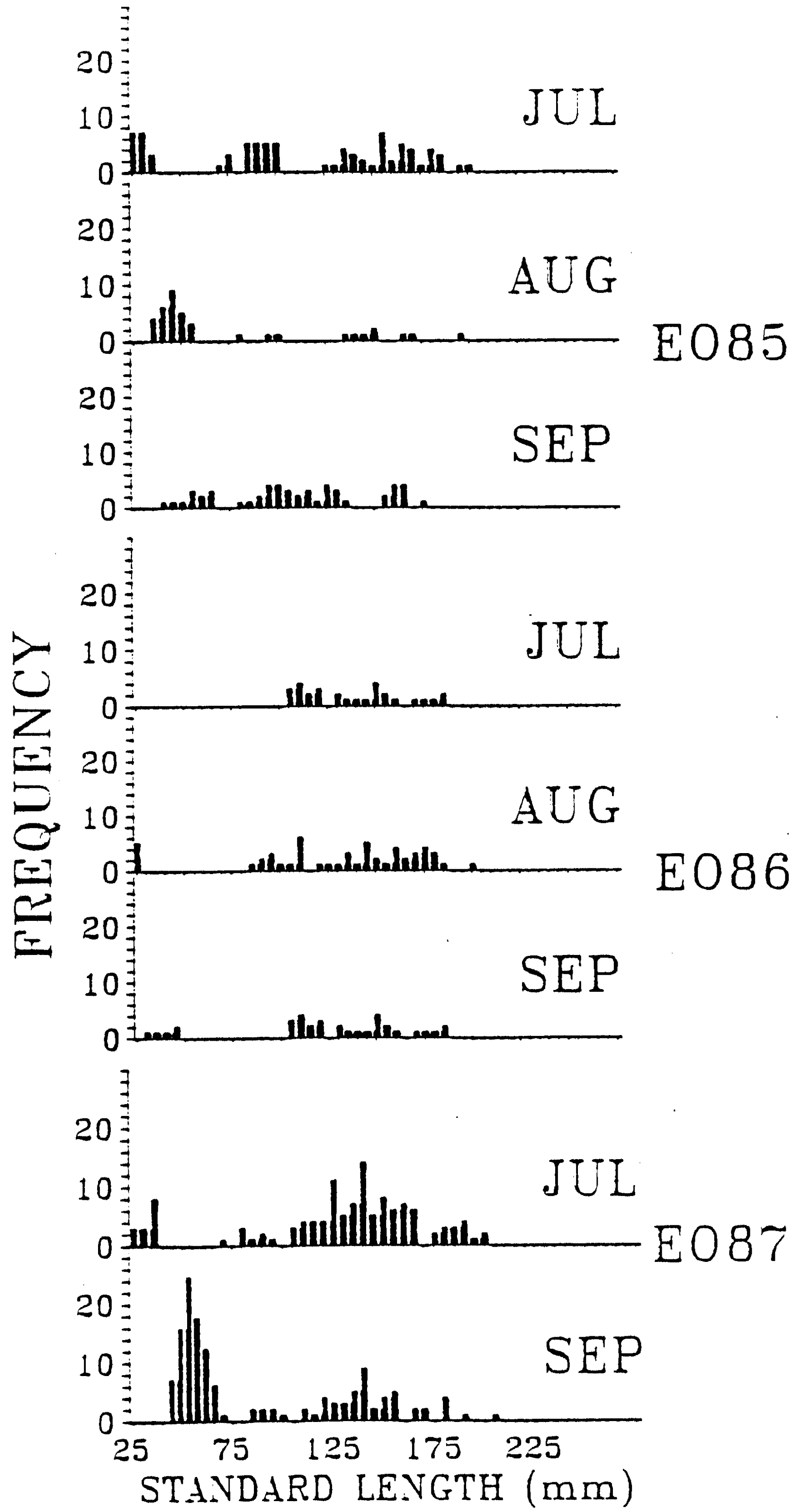


Fig. IX-10. Frequency of juvenile and adult length classes by year in Ponds 1 and 2.

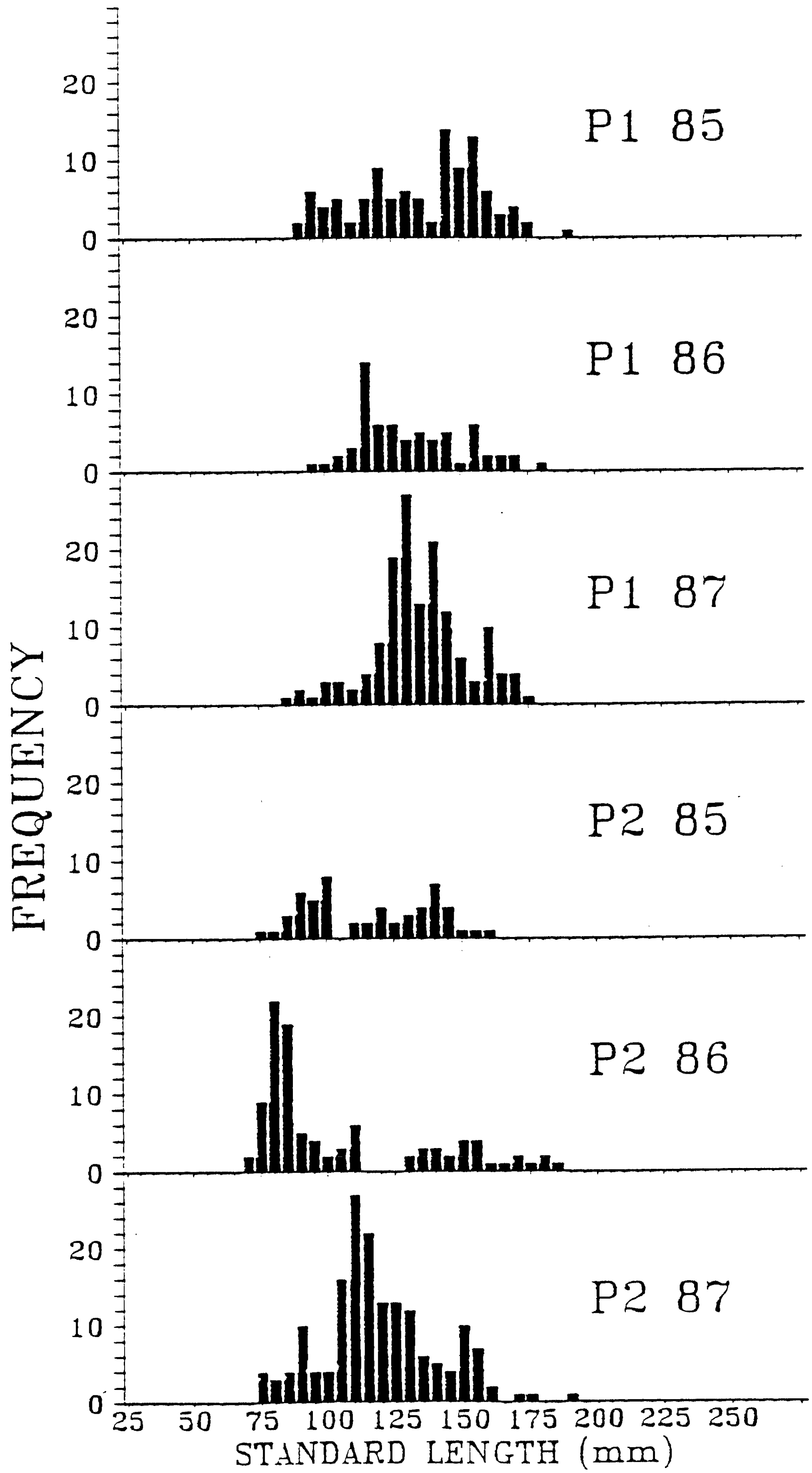


Fig. IX-11. Yearly differences in growth of 0+ brook trout in the Emerald basin. 1985-1987. Vertical lines are the 95% confidence limits.

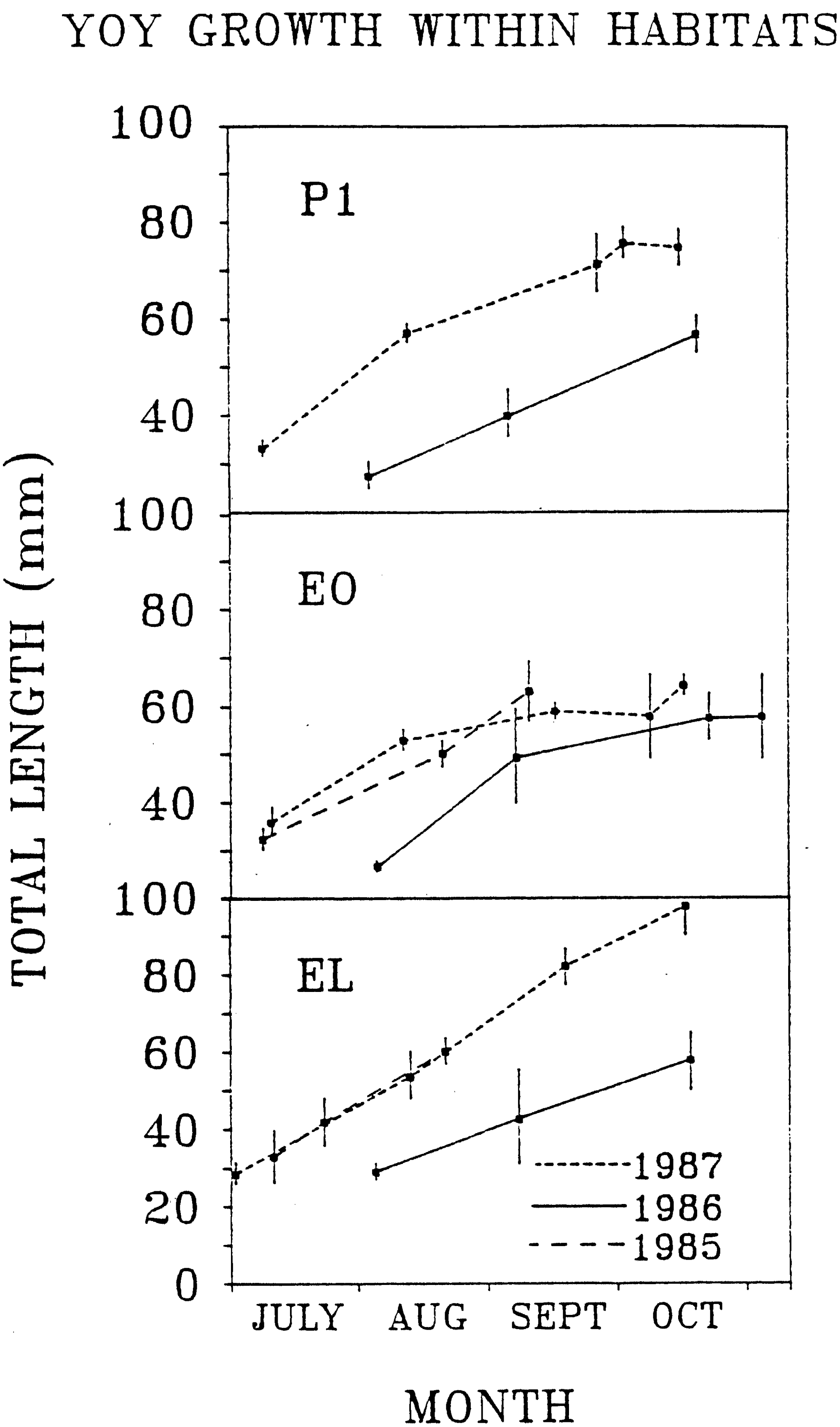


Fig. IX-12. Growth of 0+ brook trout in Emerald basin, 1985-1987, emphasizing differences among habitats. Vertical lines are 95% confidence limits.

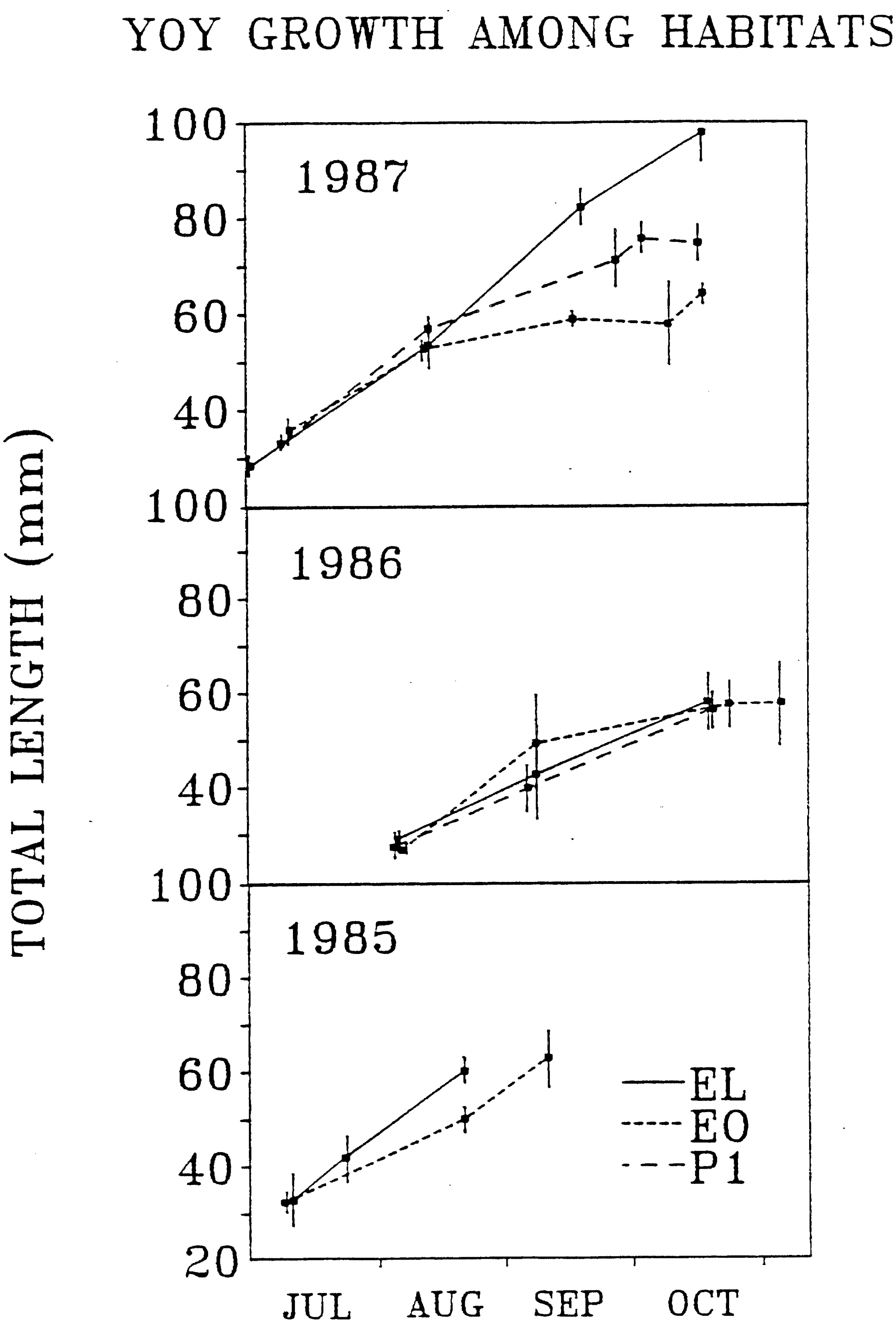


Fig. IX-13. Growth of Emerald basin brook trout. Data are combined from 1985 and 1986. Ages are from otolith rings.

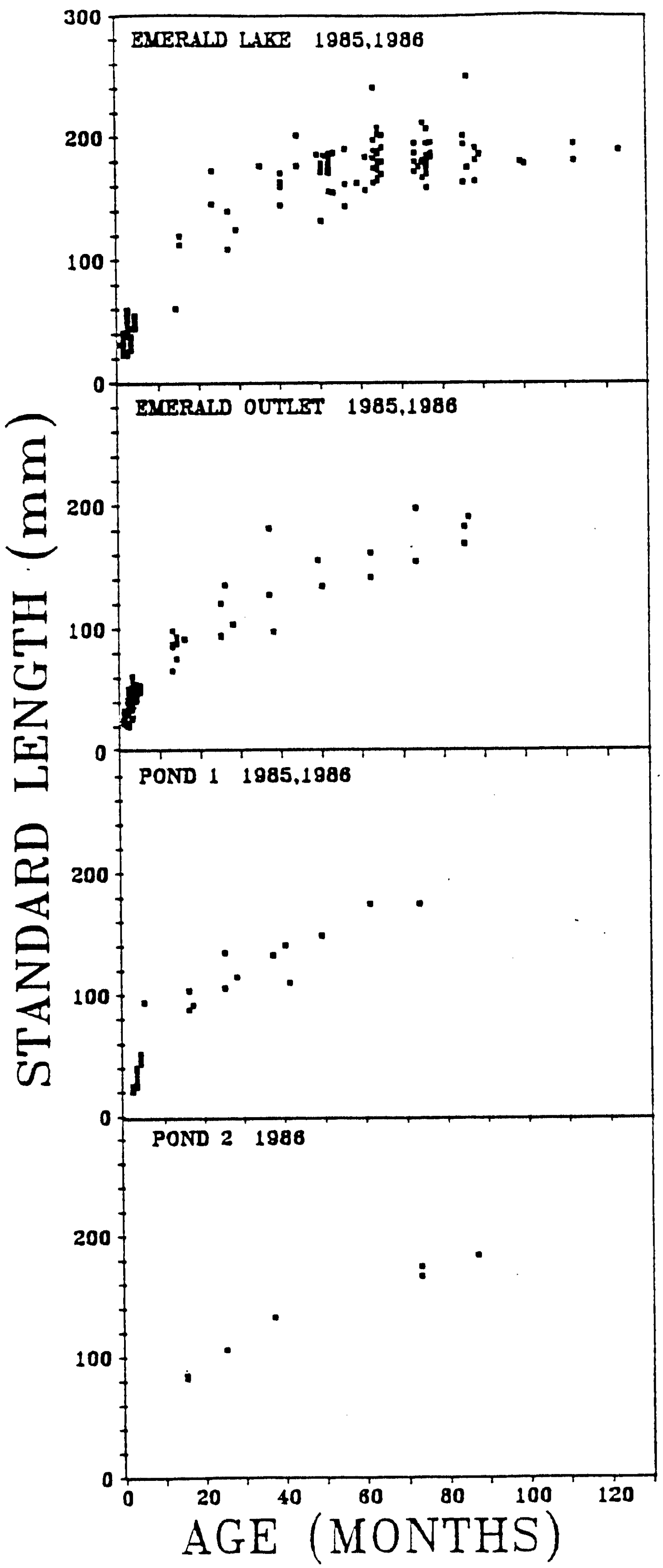


Fig. IX-14. Growth of brook trout in the 4 study lakes. Data are combined from 1985 and 1986. Ages are from otolith rings.

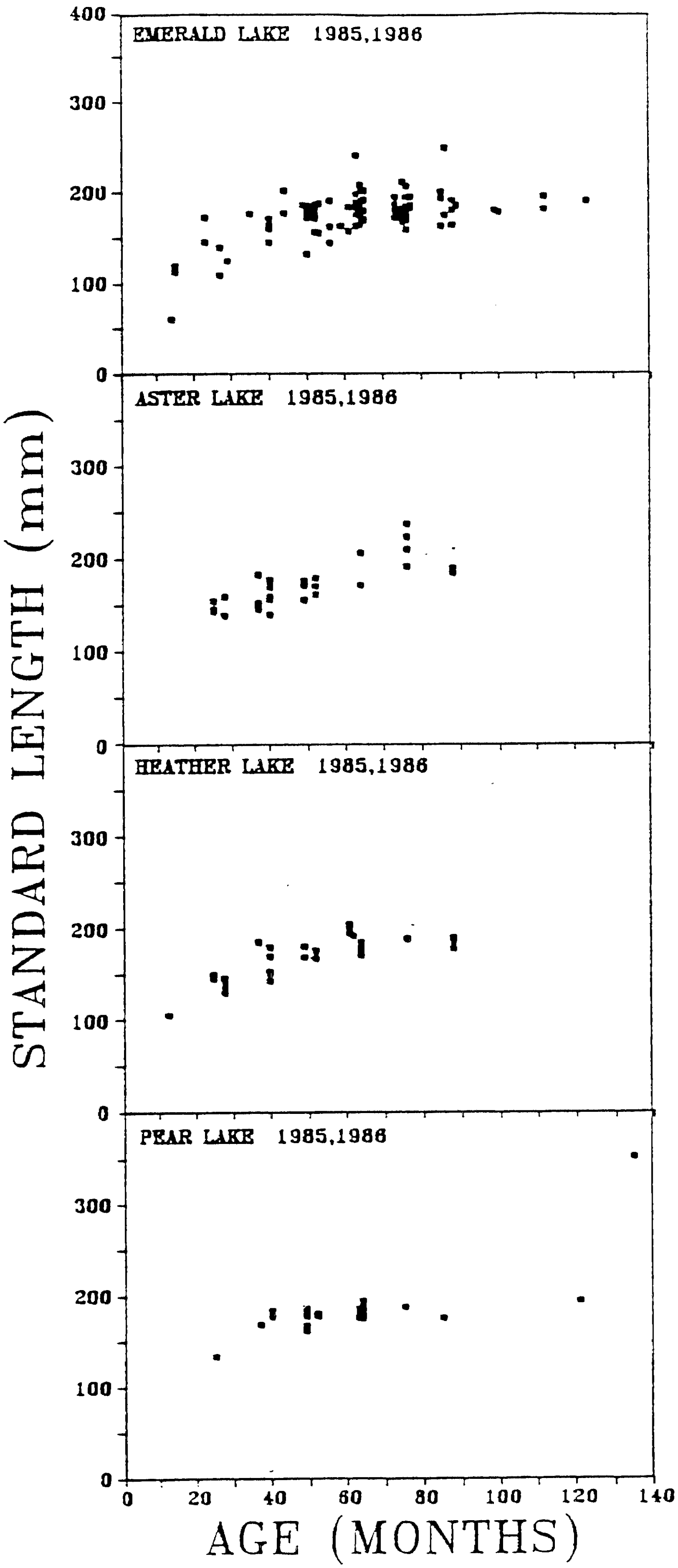


Fig. IX-15. Comparison of standard length condition factors (K) for all study waters in 1985, with means and 95% confidence intervals. $K_{sl} = (\text{Weight}/(\text{Standard Length})^3) \times 10^5$.

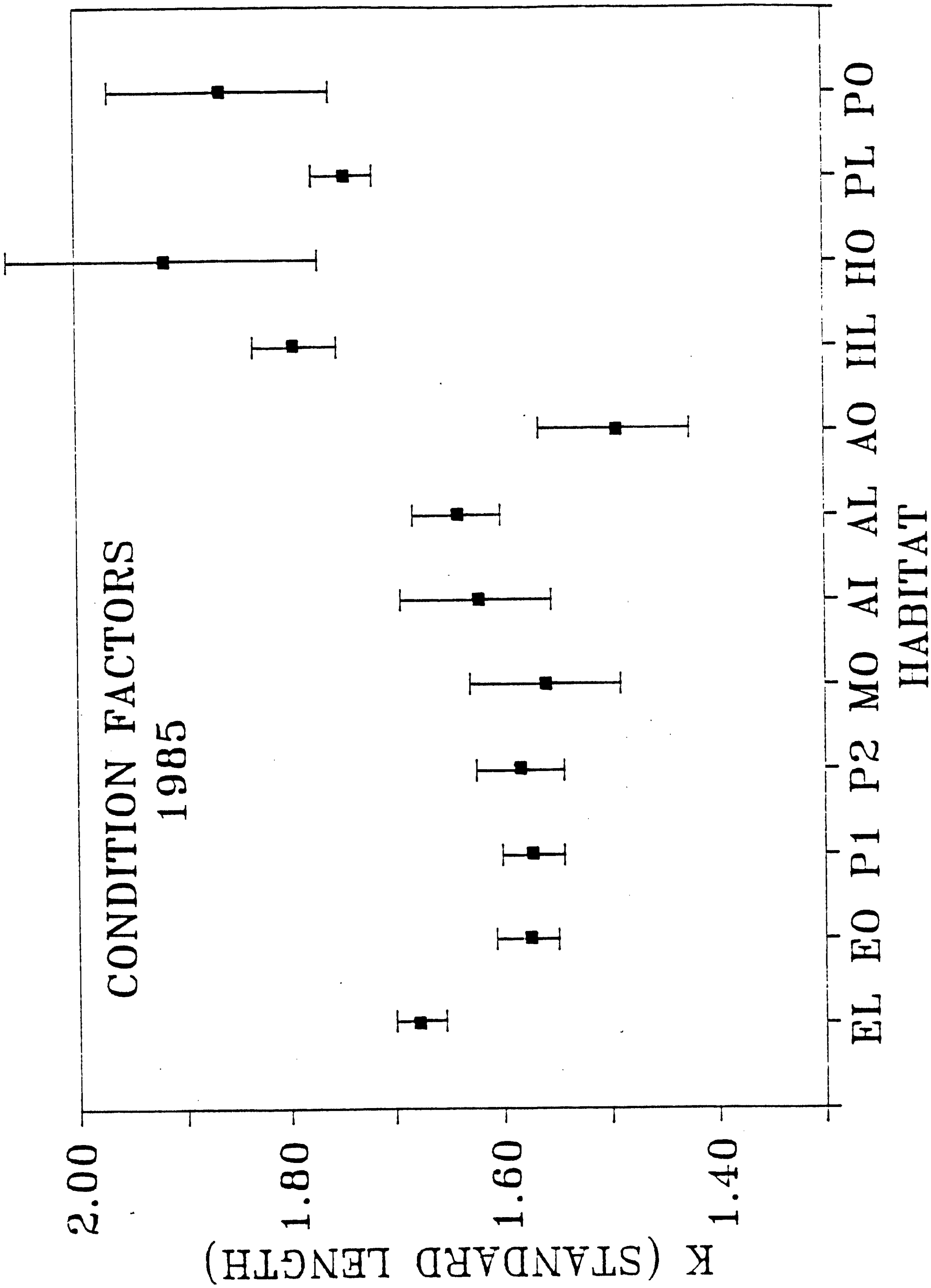


Fig. IX-16. Condition factors for brook trout in the 4 Emerald basin habitats, 1985-1987. Data are means with 95% confidence limits.

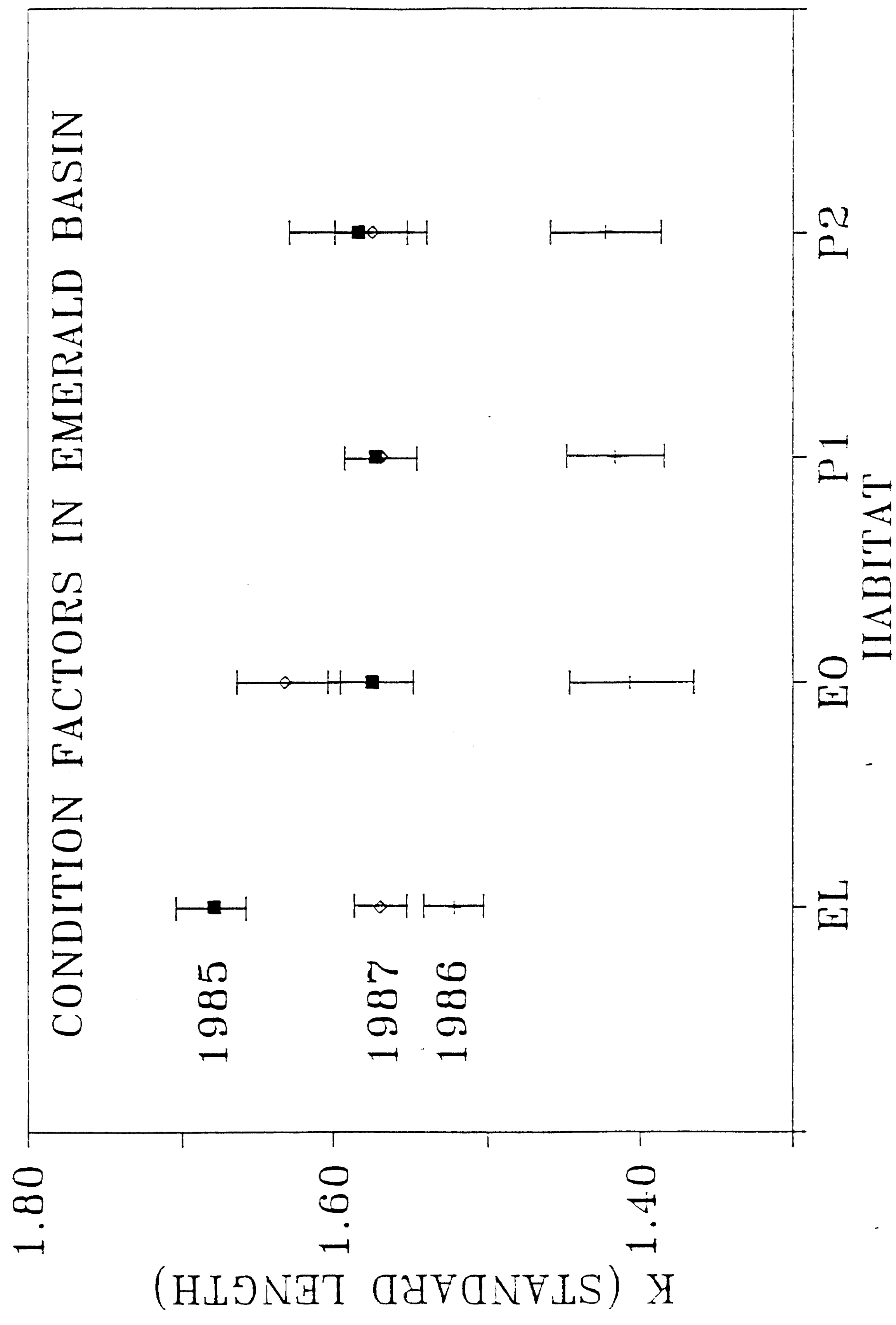
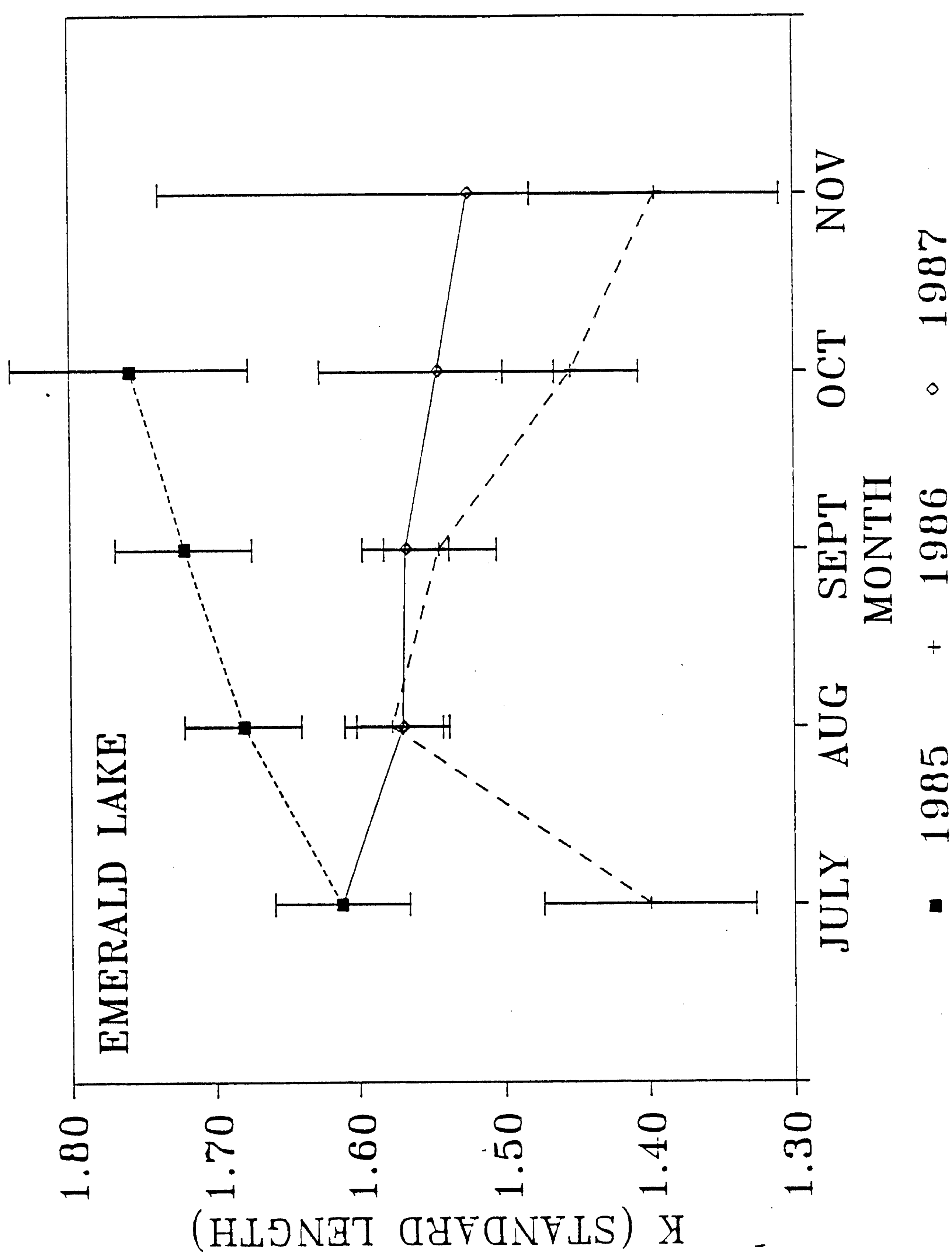


Fig. IX-17. Change in condition factors of brook trout in Emerald Lake during summer and fall, 1985-1987. Means and 95% confidence limits.



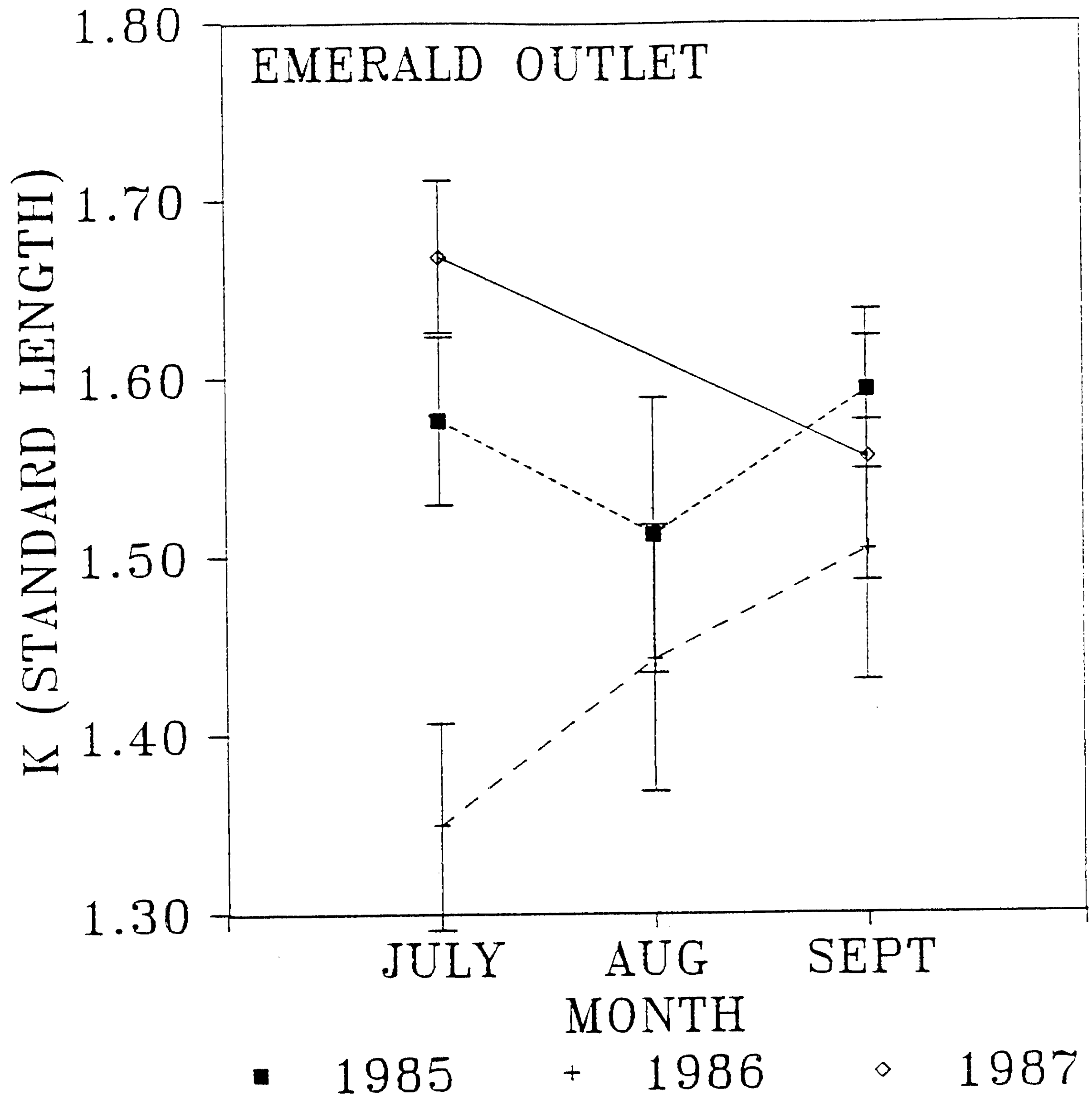


Fig. IX-18. Change in condition factors of brook trout in Emerald outlet during summer and fall, 1985-1987. Means and 95% confidence limits.

Fig. IX-19. Relationship between body lipid and water content of all brook trout analyzed in 1985 and 1986. Includes least squares regression line ($Y = -0.44x + 36.5$, $r^2 = 0.72$, $n = 66$).

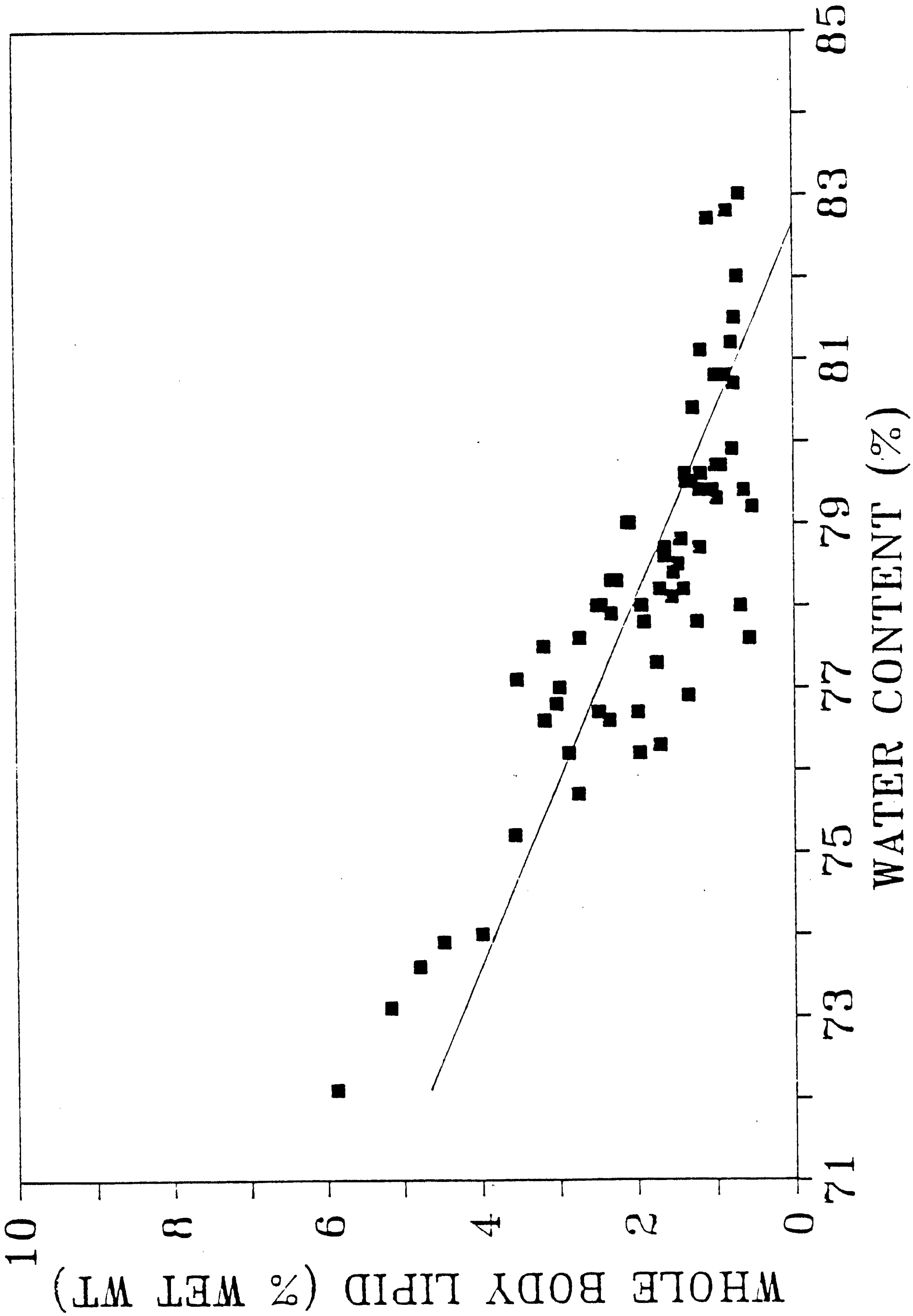


Fig. IX-20. Whole body lipid content of brook trout from the 4 study lakes. Bars are ± two standard errors.

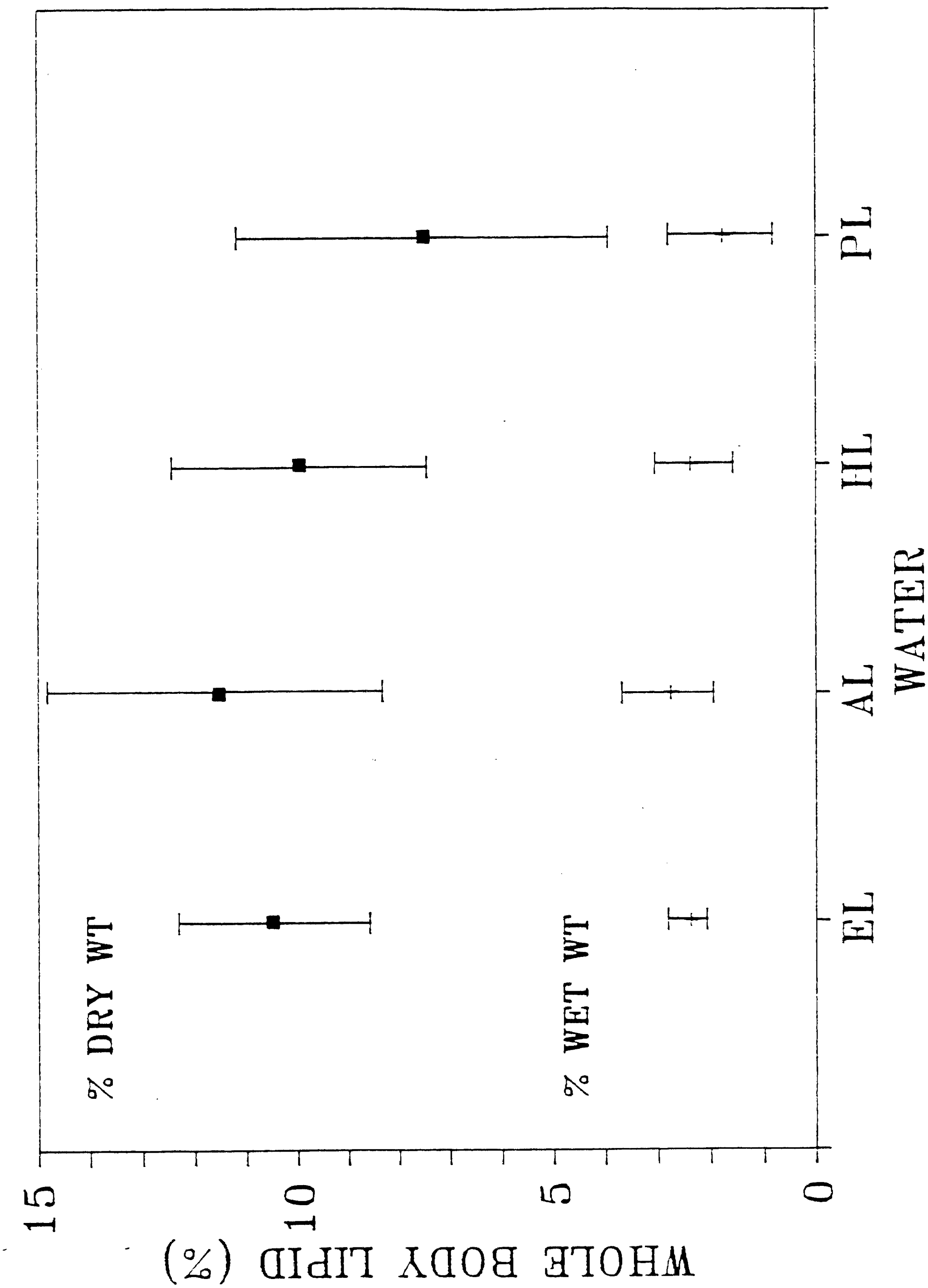


Fig. IX-21. Temporal changes in the gonad weight/body weight ratio (GSI) for males and females in Emerald Lake. Bars denote ± two standard errors.

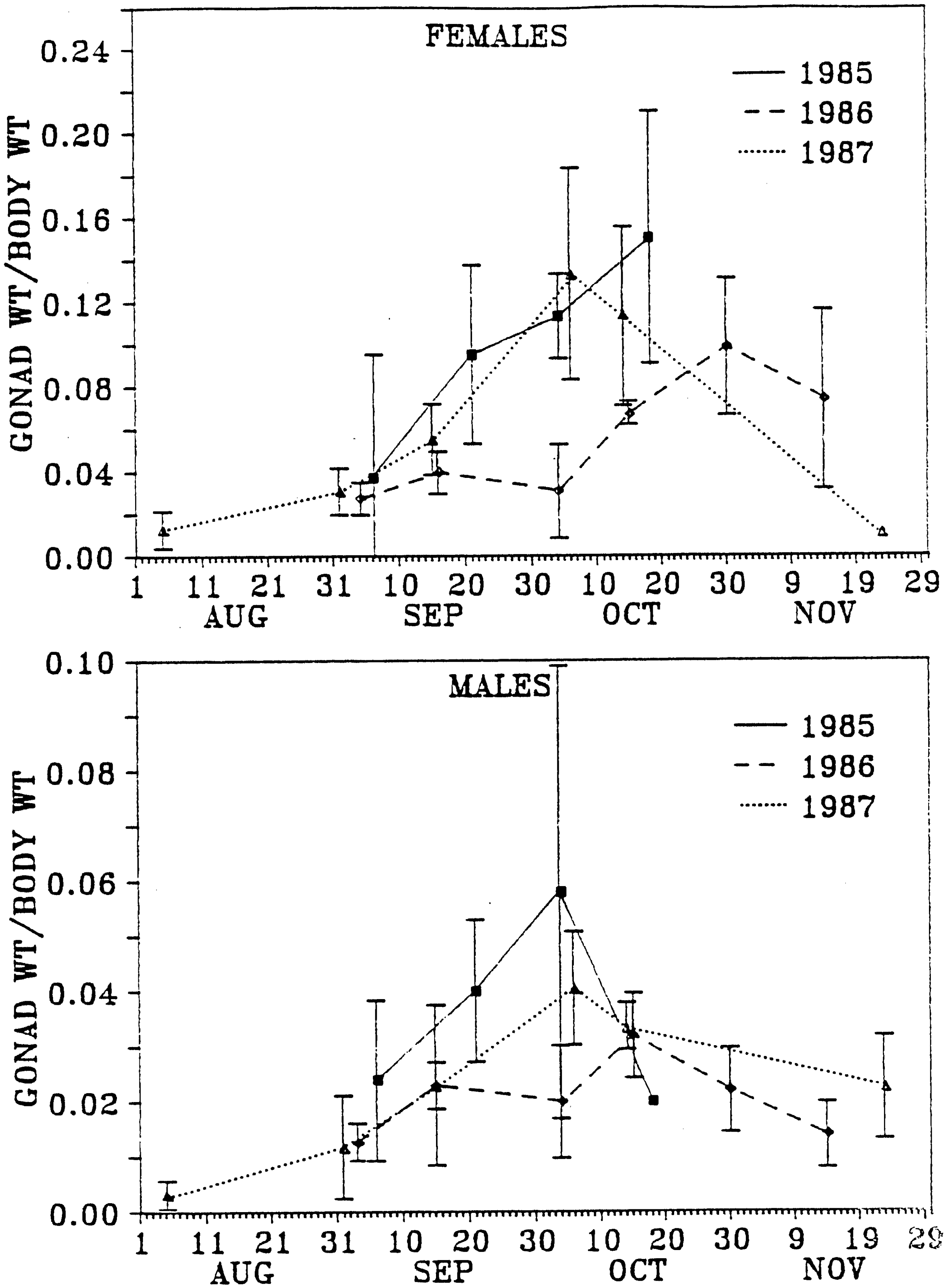


Fig. IX-22. Comparisons among 1985, 1986 and 1987 female brook trout gonad weight/body weight ratios in Marble Fork waters. Data are means with 95% confidence limits. All samples from Heather, Pear and Aster Lakes were taken between 30 Sep-19 Oct. Pond 1 fish were taken between 3-10 Oct. Pond 2 fish were taken on 18 Sep (1986) and 15 Sep (1987). Emerald Lake samples were taken between 21 Sep-18 Oct, 16 Sep-14 Nov, and 15 Sep-15 Oct in 1985, 1986 and 1987, respectively.

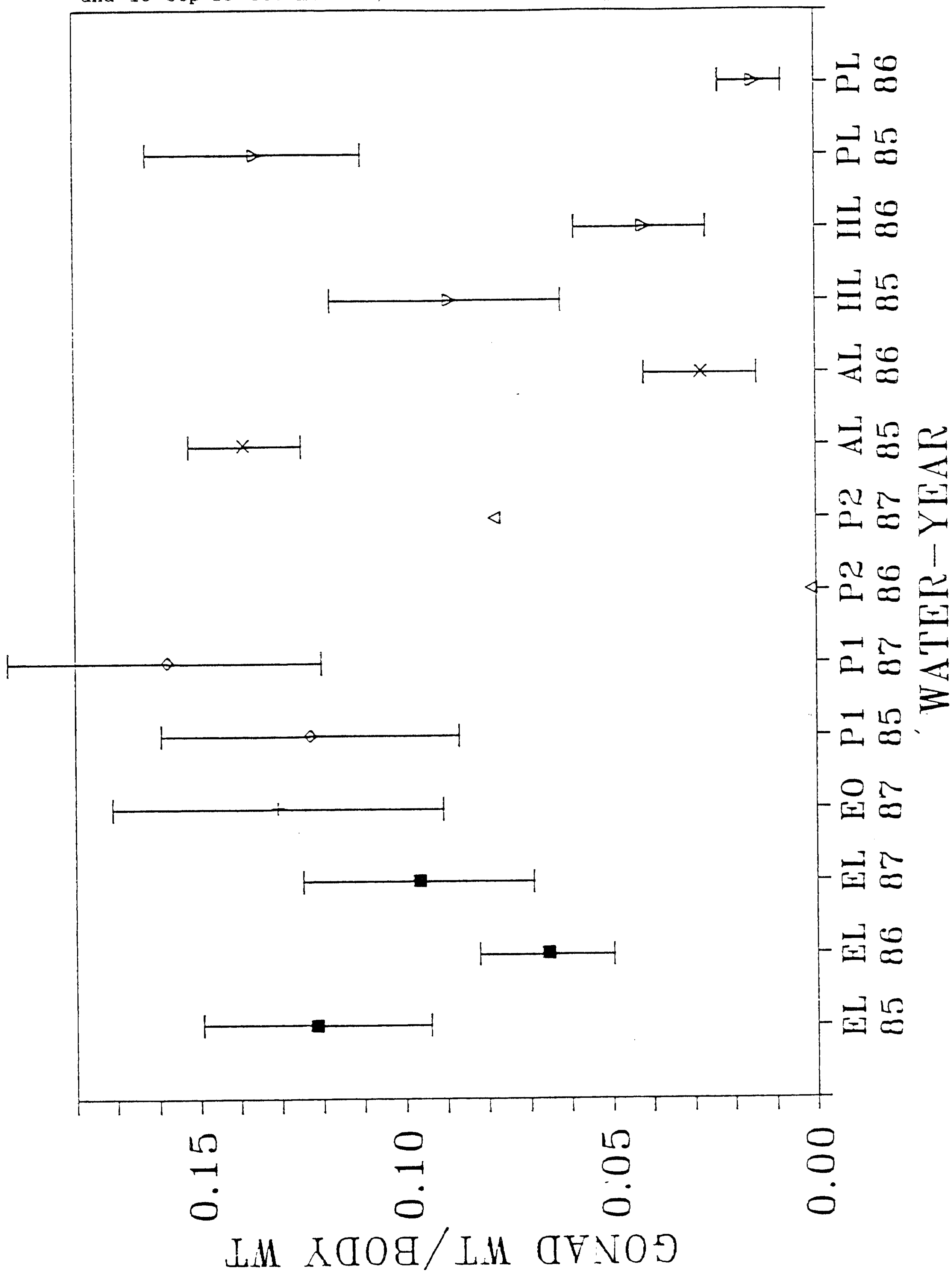


Fig. IX-23. Comparison of number of eggs per ovary in several waters during the 1985, 1986 and 1987 reproductive seasons. Means and 95% confidence limits.

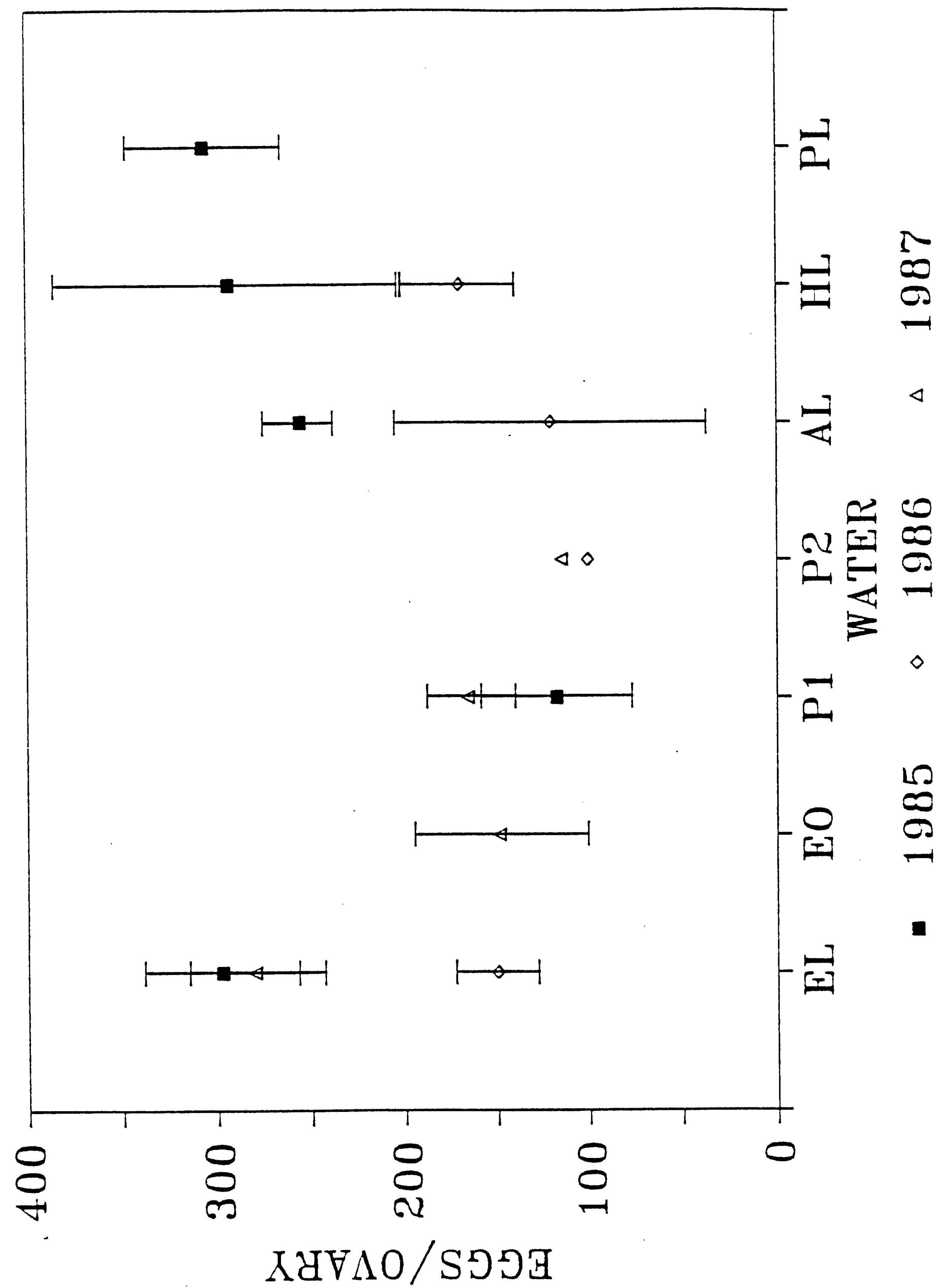


Fig. IX-24. Comparison of 1985, 1986 and 1987 egg diameters for brook trout in several study waters. Means and 95% confidence limits.

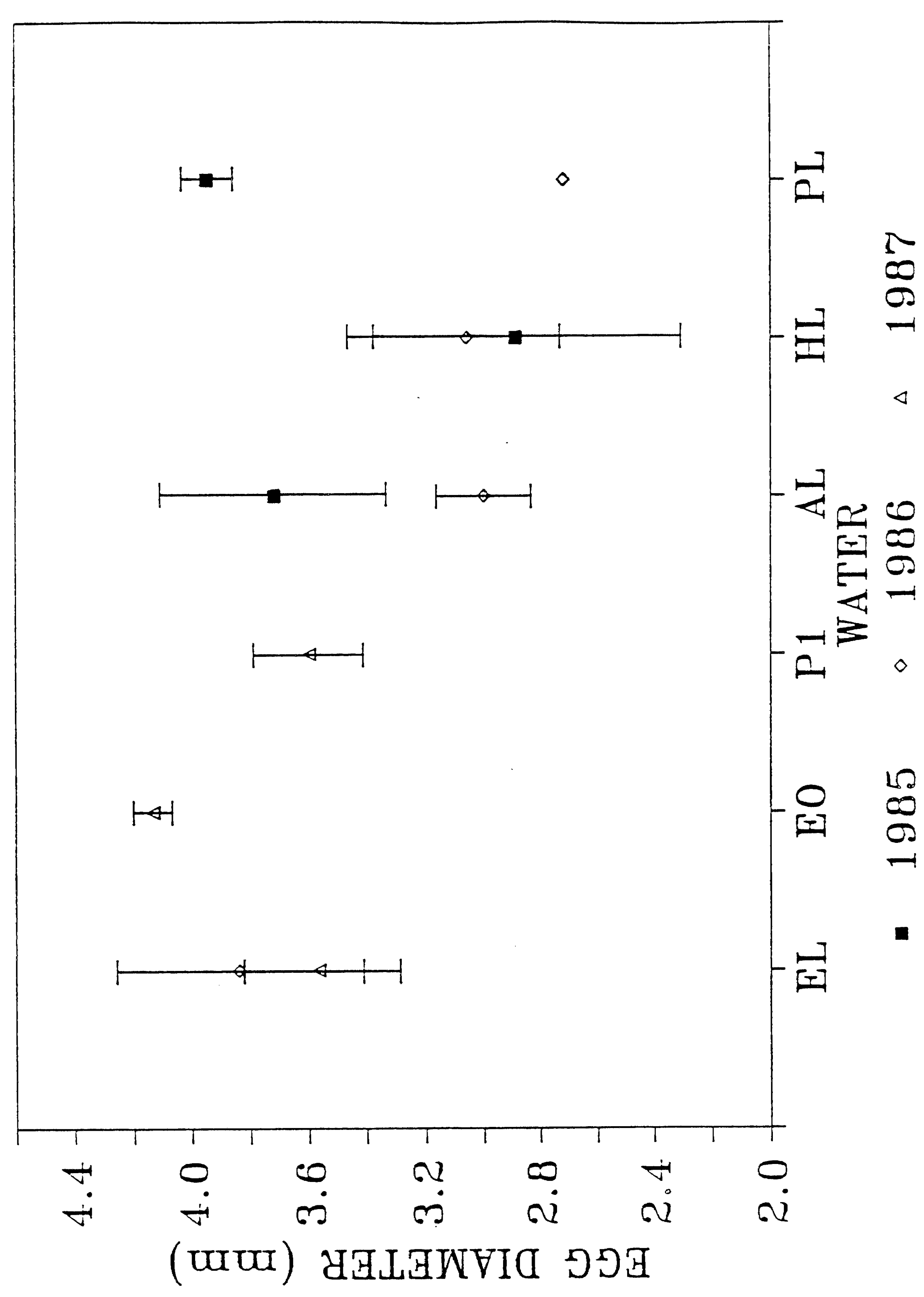


Fig. IX-25. Timing of 1985 spawning runs in the Emerald Lake basin relative to changes in temperature and stream discharge.

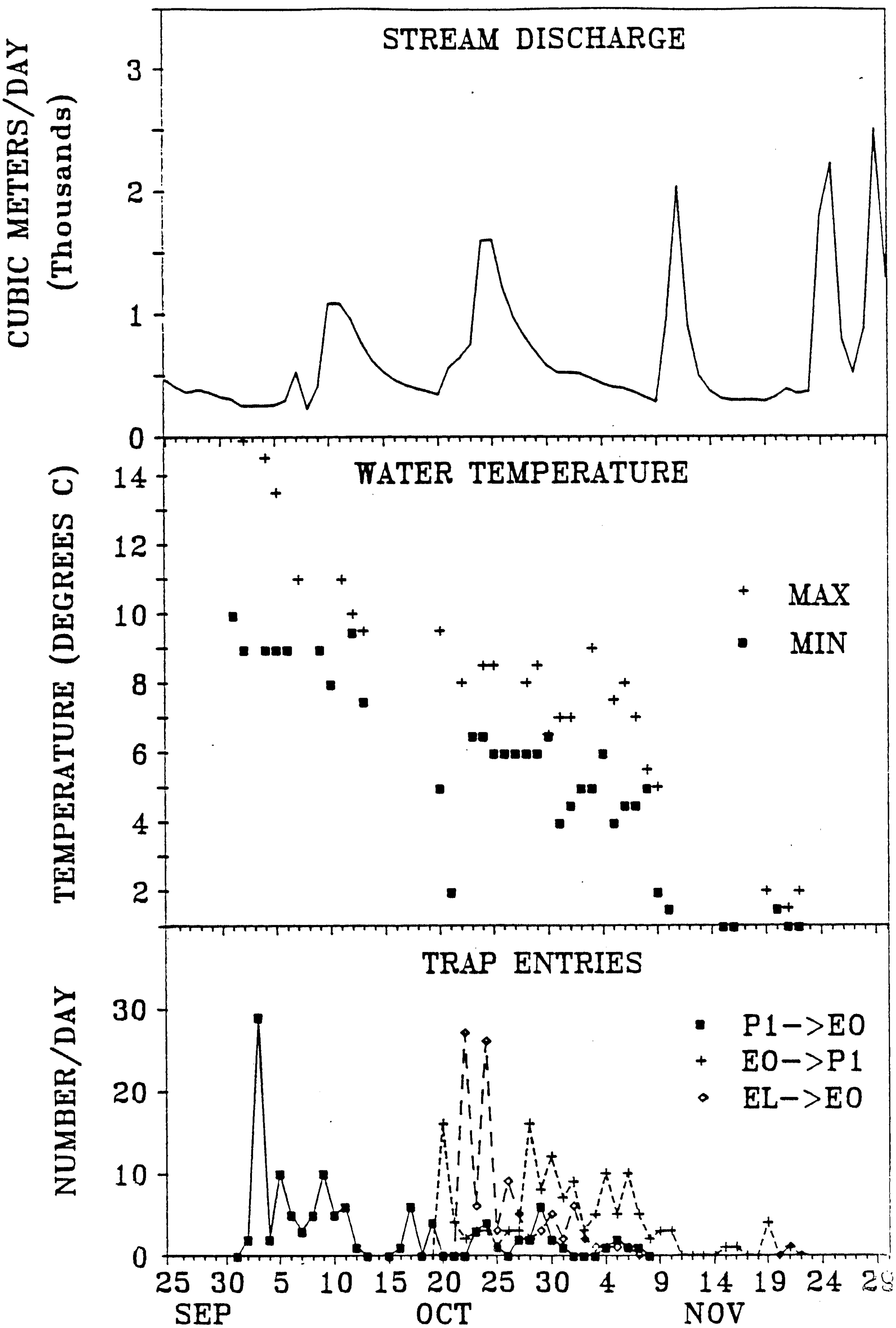


Fig. IX-26. Timing of 1986 spawning runs in the Emerald Lake basin relative to changes in temperature and stream discharge.

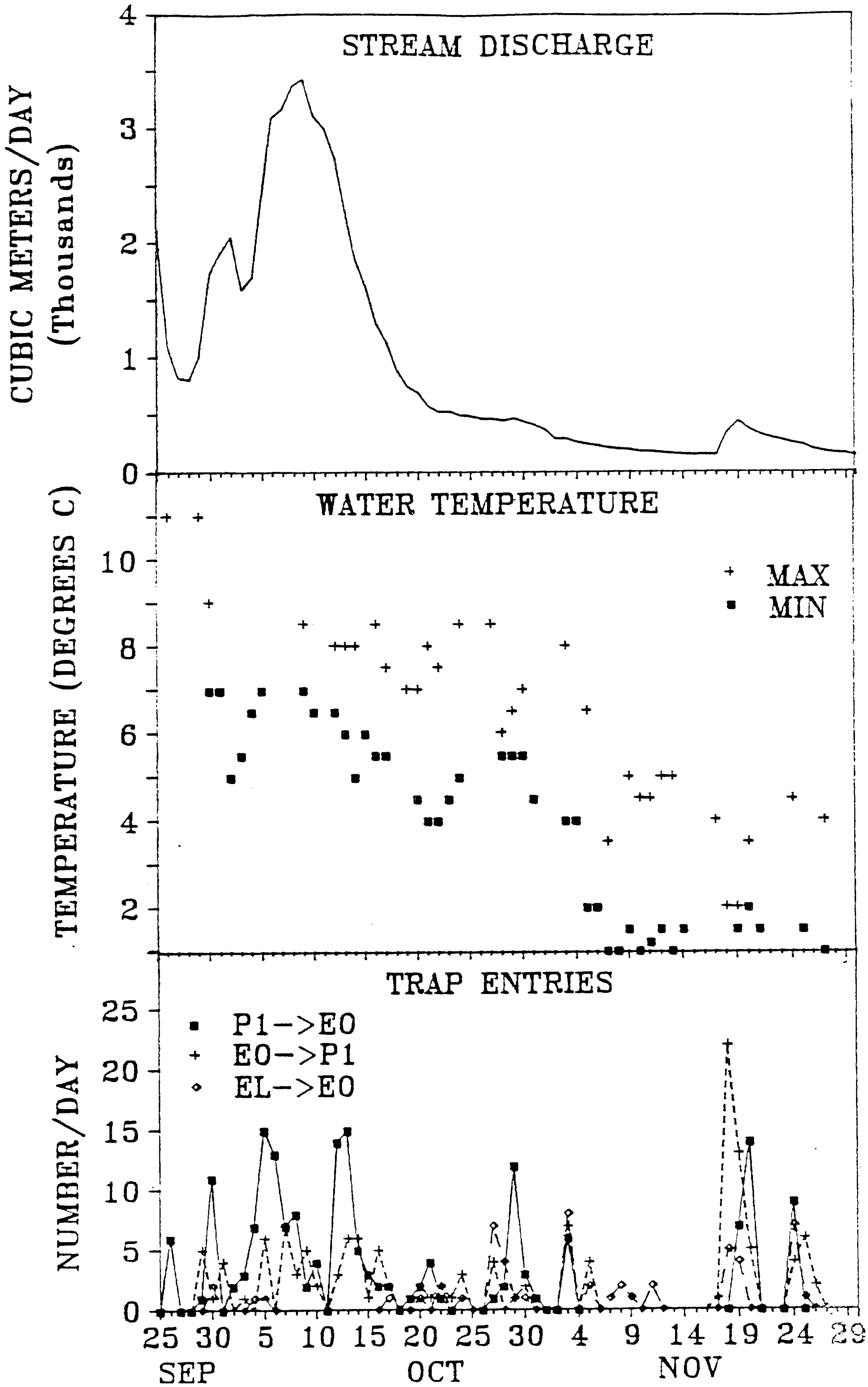


Fig. IX-27. Timing of 1987 spawning runs in the Emerald Lake basin relative to changes in temperature and stream discharge.

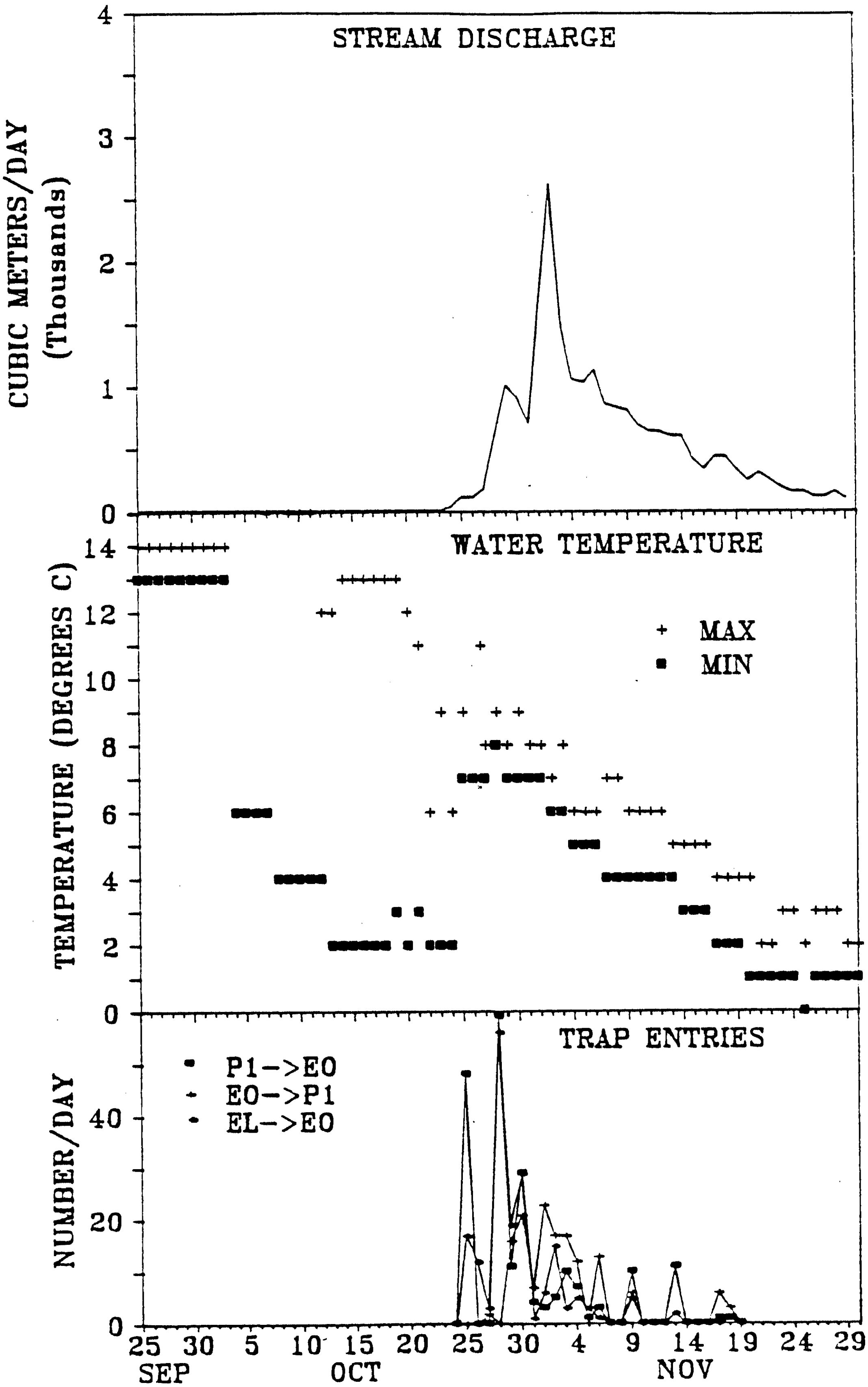
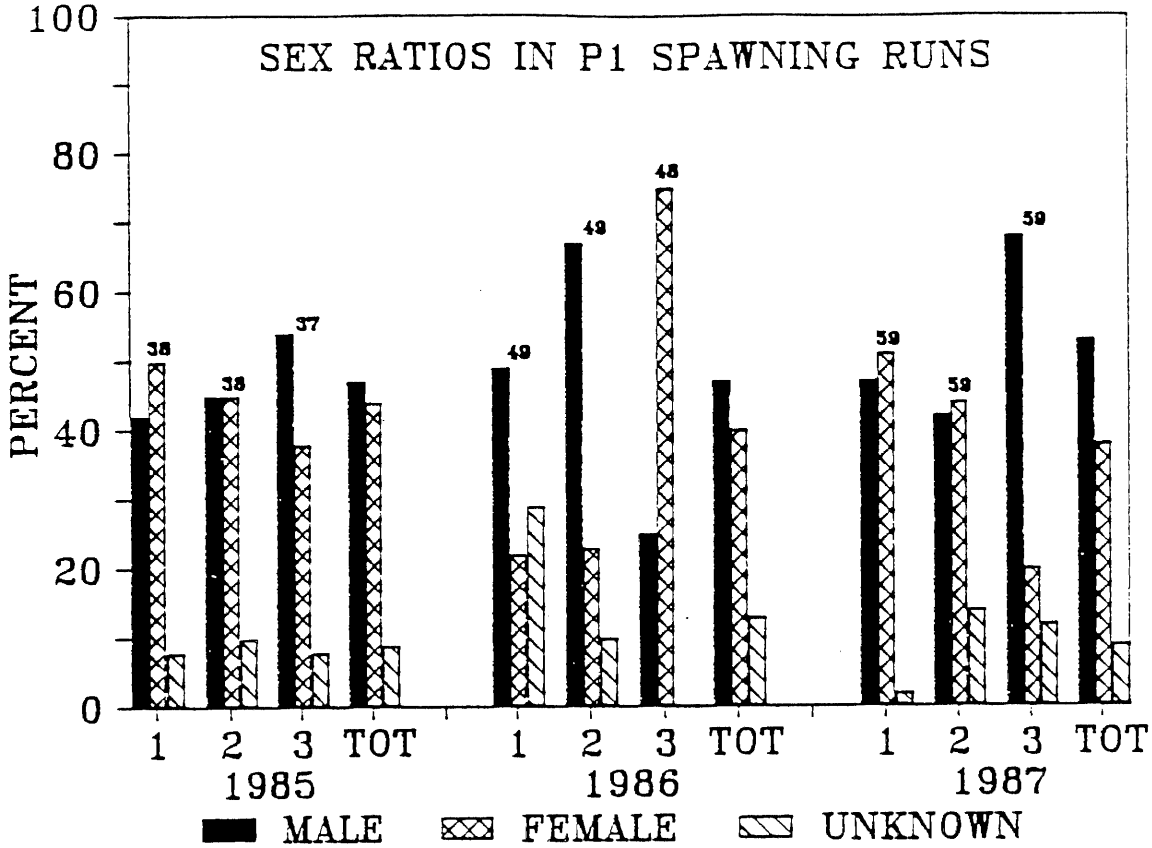


Fig. IX-28. Sex ratio of brook trout entering Emerald outlet from Pond 1 and Emerald Lake during the 1985-1987 spawning seasons. 1 = first third of trap entrants, 2 = second third, and 3 = last third. Numbers above bars are males + females.



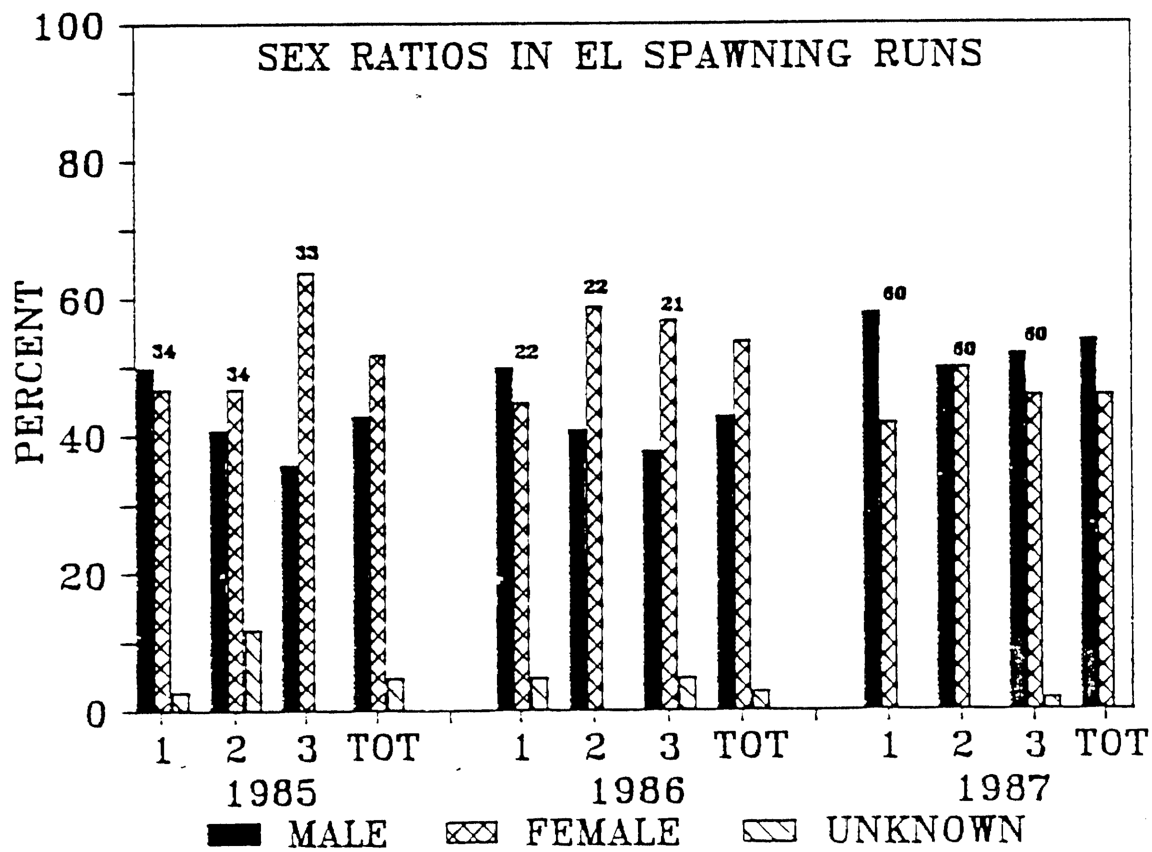


Fig. IX-29. Summary of spawning and egg production in the Emerald outlet during the 1985, 1986 and 1987 reproductive seasons.

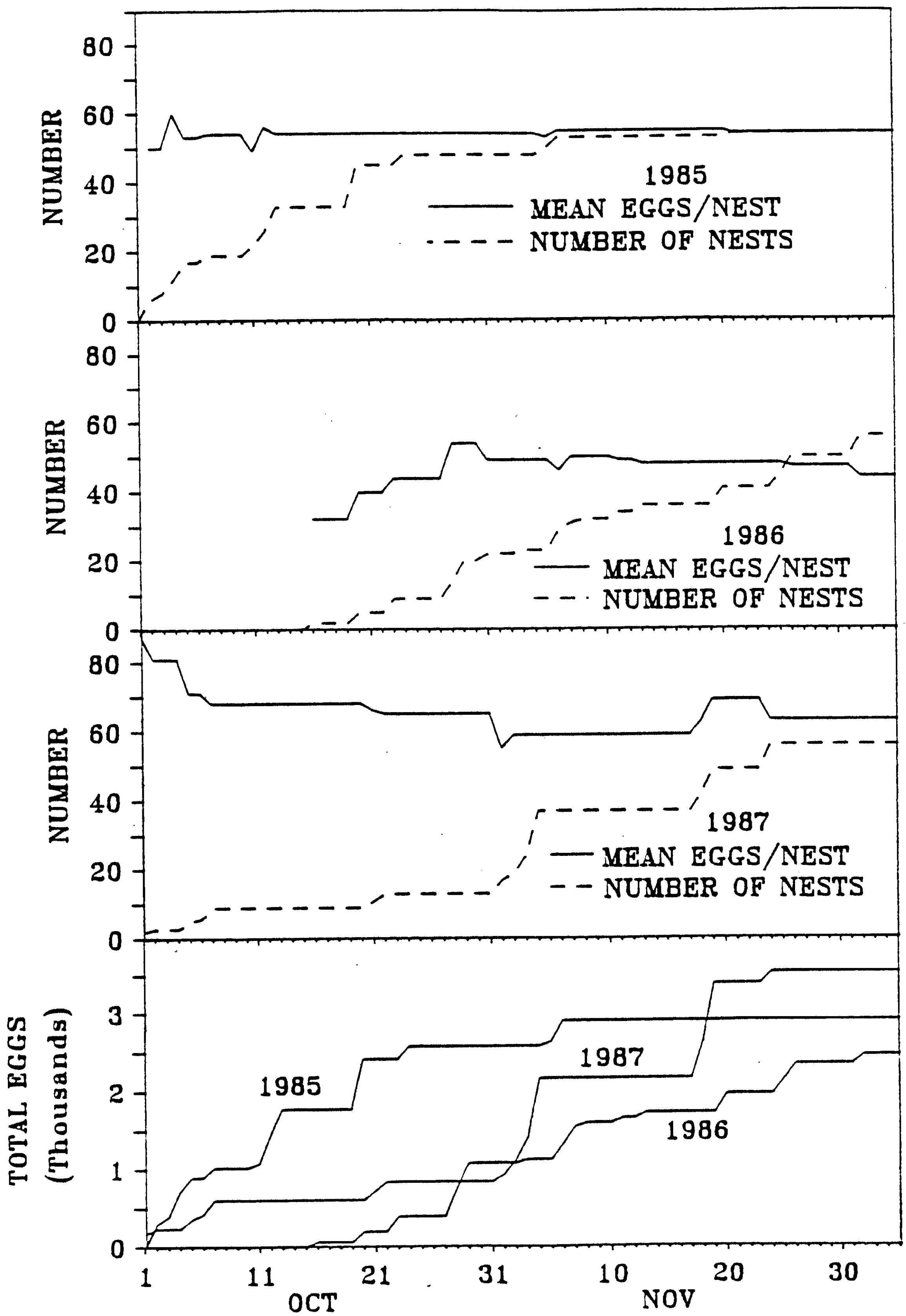


Fig. IX-30. Timing of embryo development in nine 6-pack modules during the 1985-1986 reproductive seasons. Solid lines represent pre-hatching development; rectangles represent the duration of hatching (open rectangles show when an experiment was terminated before hatching ceased); broken lines show period from hatching to emergence; dotted lines represent newly emerged fry.

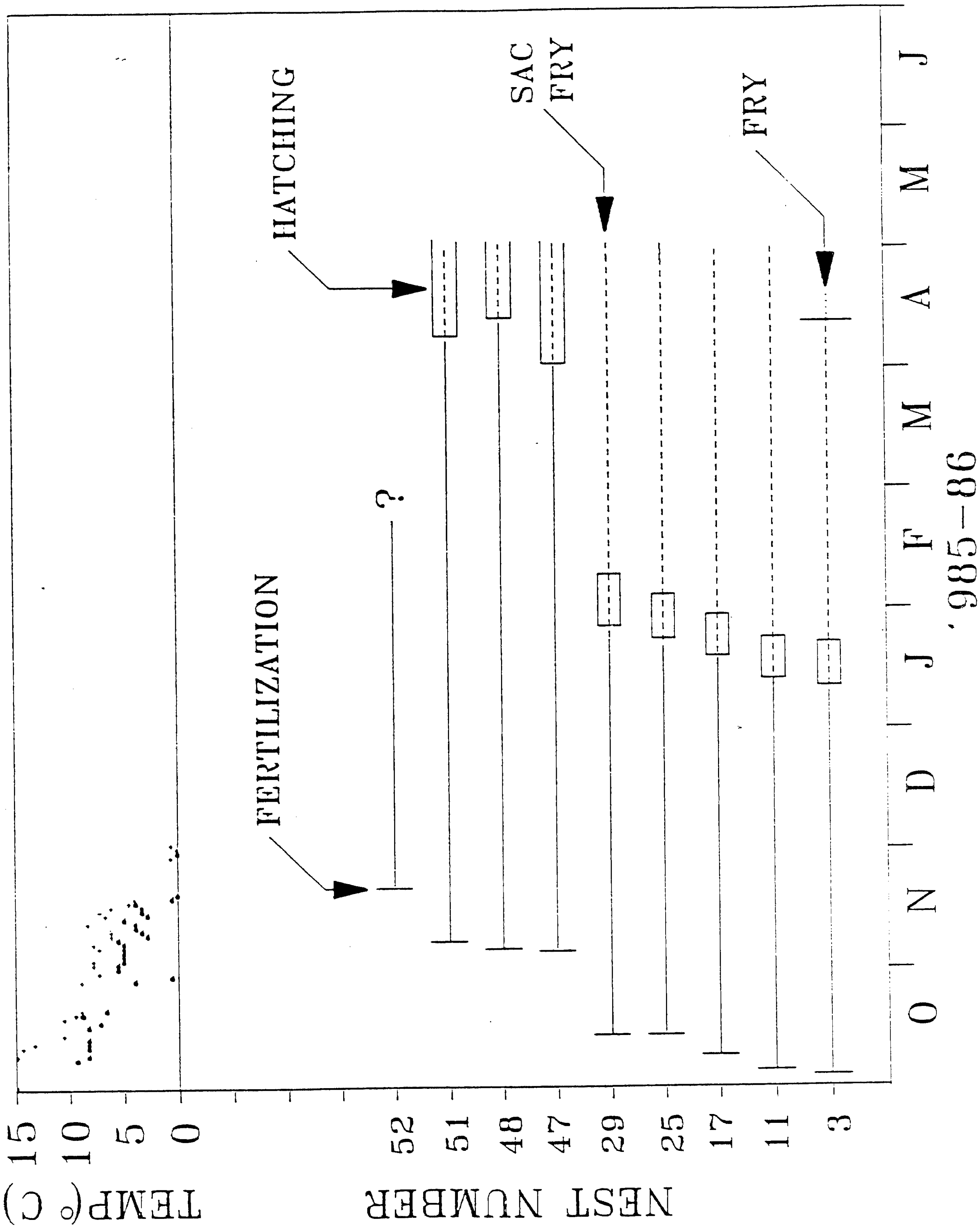


Fig. IX-31. Timing of embryo development in twelve 6-pack modules during the 1986-1987 reproductive season. Symbols as in Fig. IX-30, but solid circles indicate total mortality of embryos before hatching.

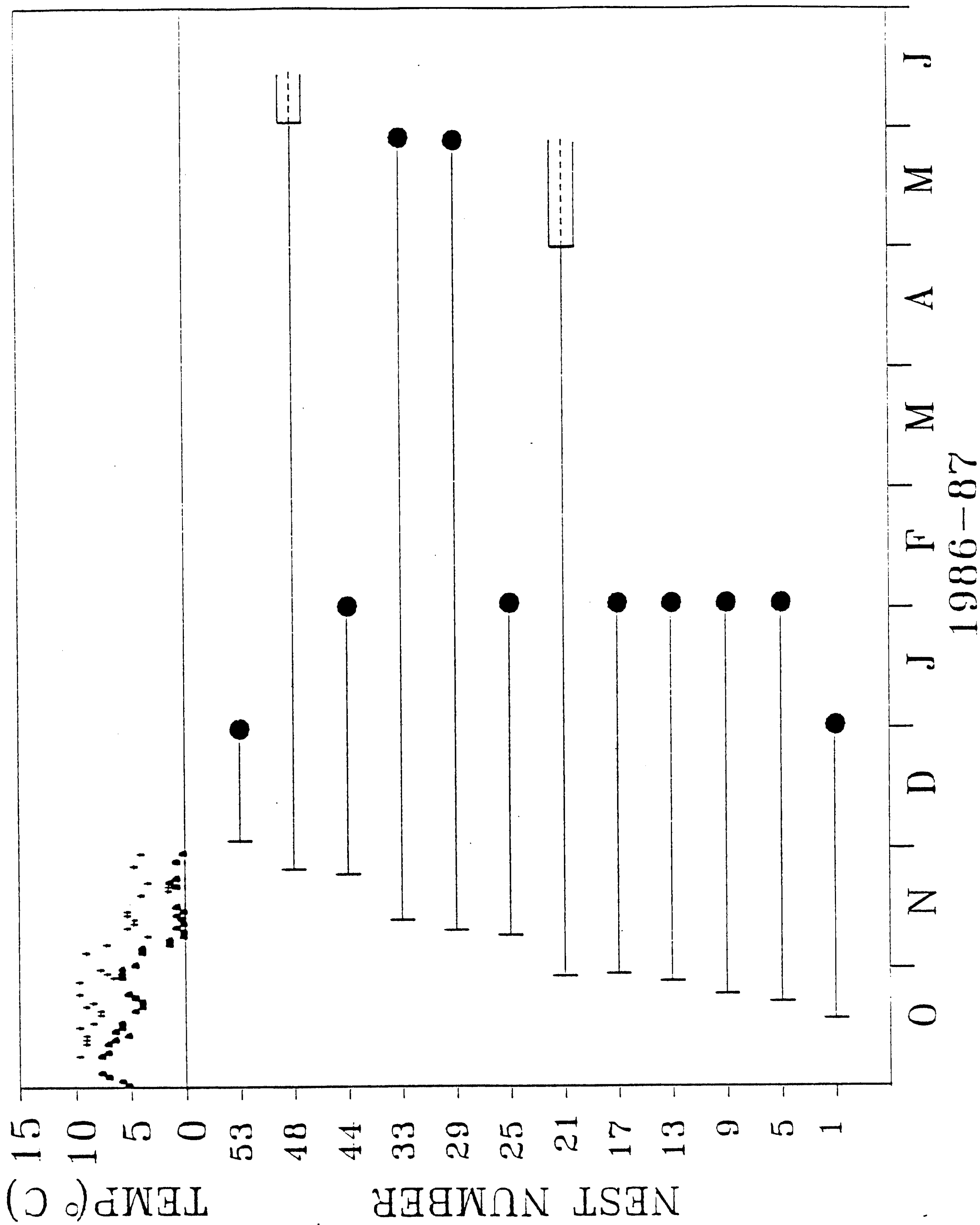


Fig 32. Timing of embryo development in eleven 6-pack modules during the 1987-1988 reproductive season. The twelfth module was inundated by rising waters and could not be recovered without diving under the ice. Symbols as in Figs. 30, 31.

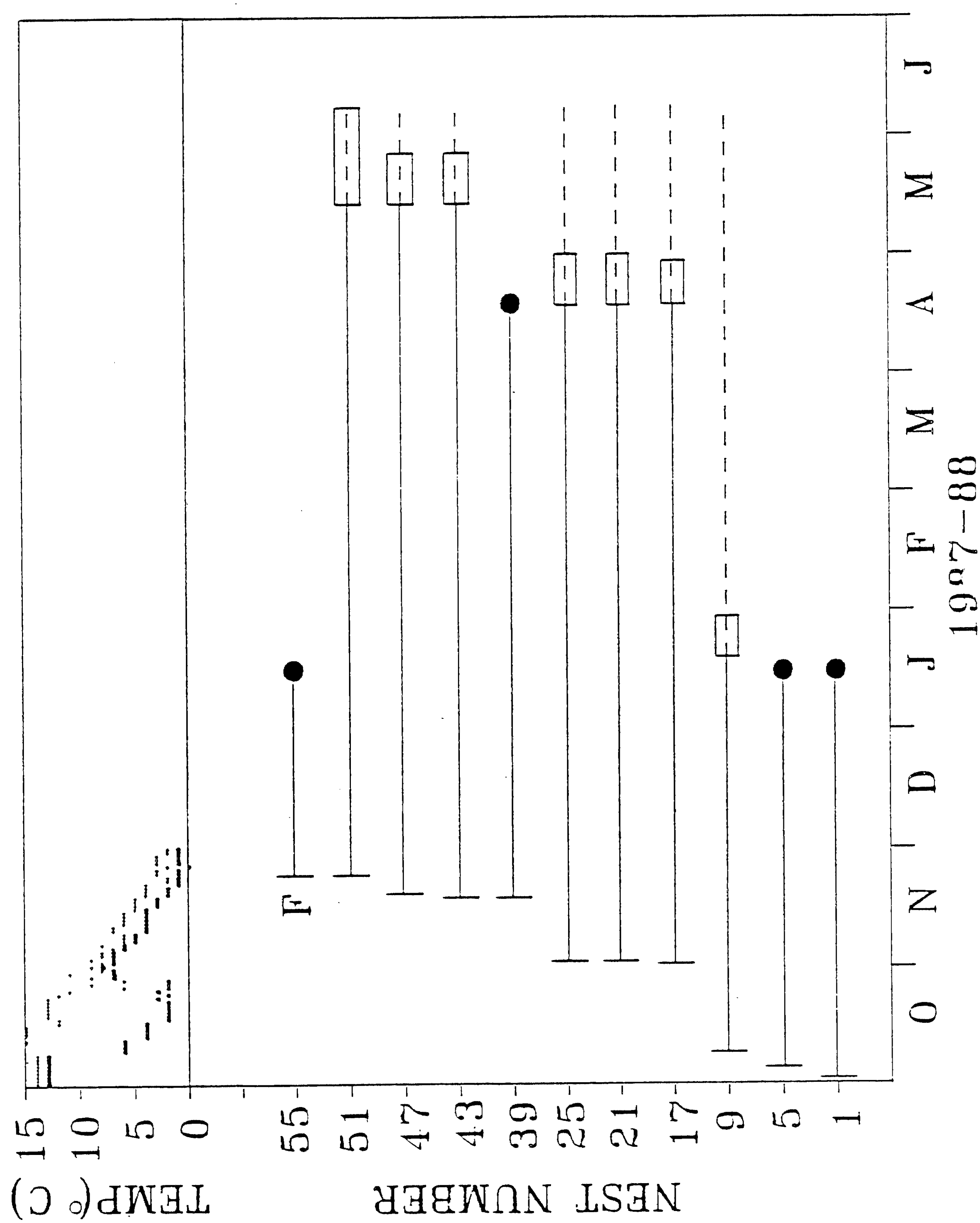


Fig. IX-33. Mean numbers of prey in the stomachs of adult fish in Emerald Lake during sampling periods from Jul 1985-Oct 1987. Vertical lines are 95% confidence intervals. Numbers above bars are sample sizes.

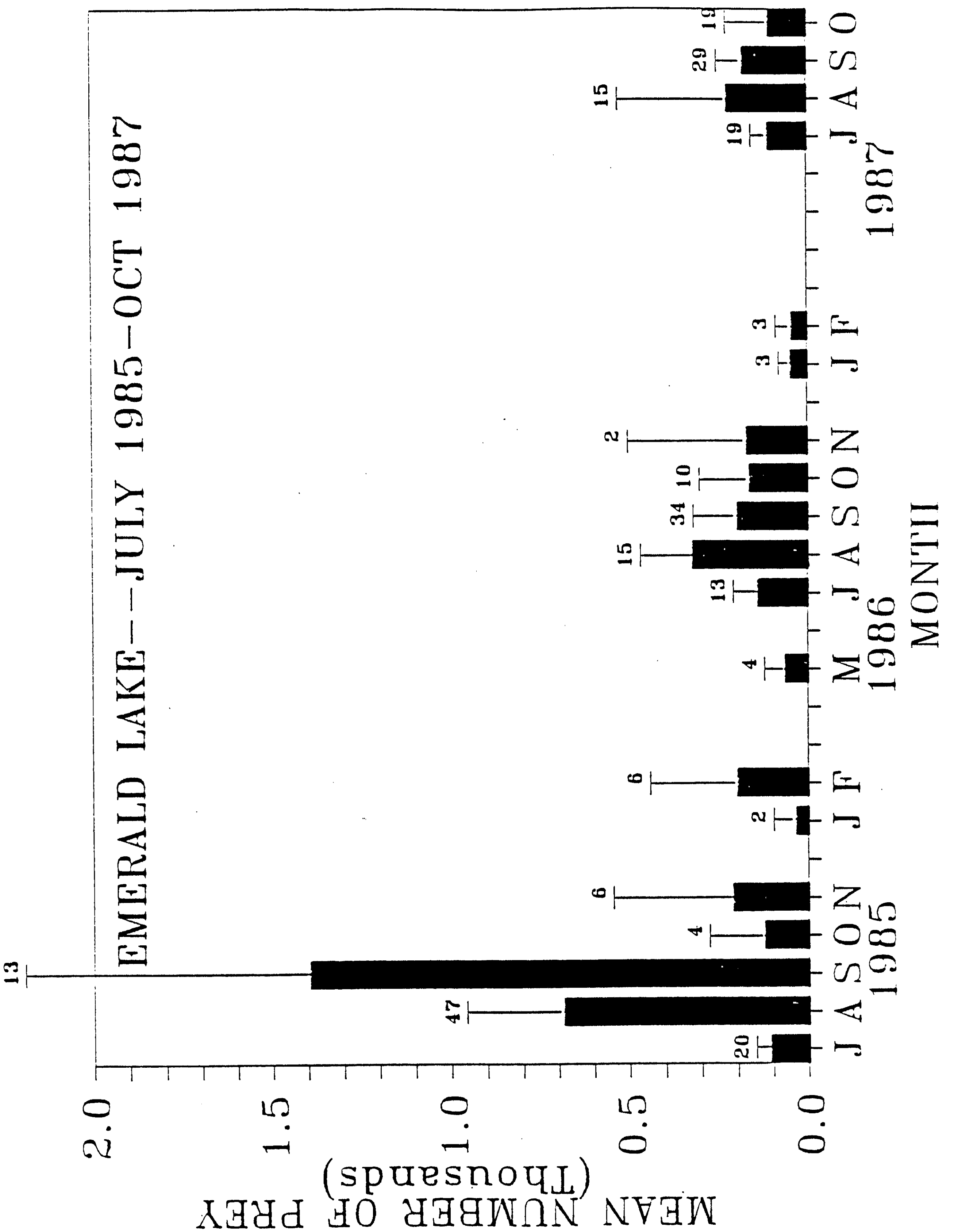


Fig. IX-34. Mean numbers of prey in the stomachs of 0+ brook trout in Emerald Lake, 1985-1987. Vertical lines are 95% confidence intervals. Numbers above bars are sample sizes.

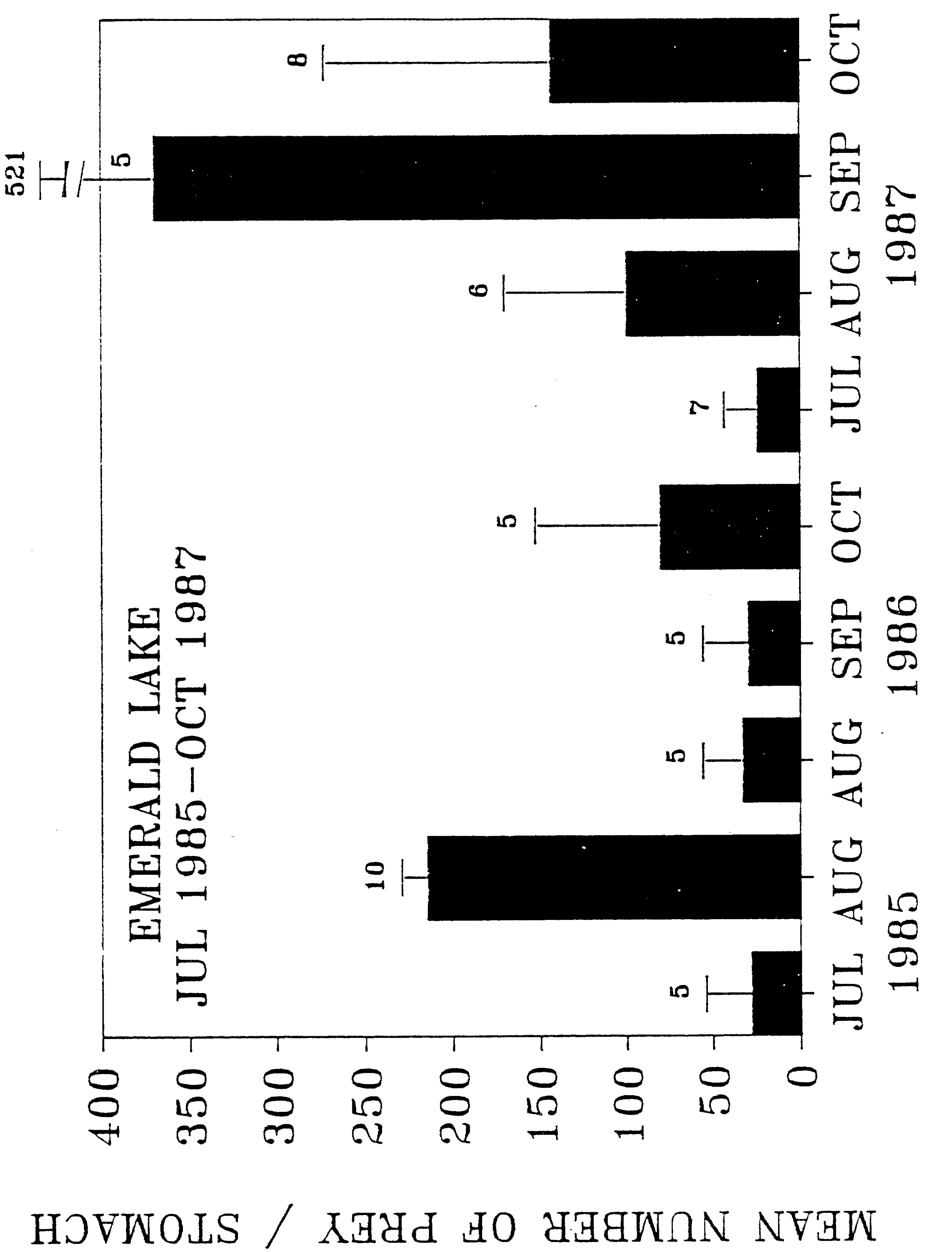


Fig. IX-35. Mean numbers of prey in the stomachs of adult fish from Aster, Heather and Pear lakes during sampling periods in 1985 and 1986.

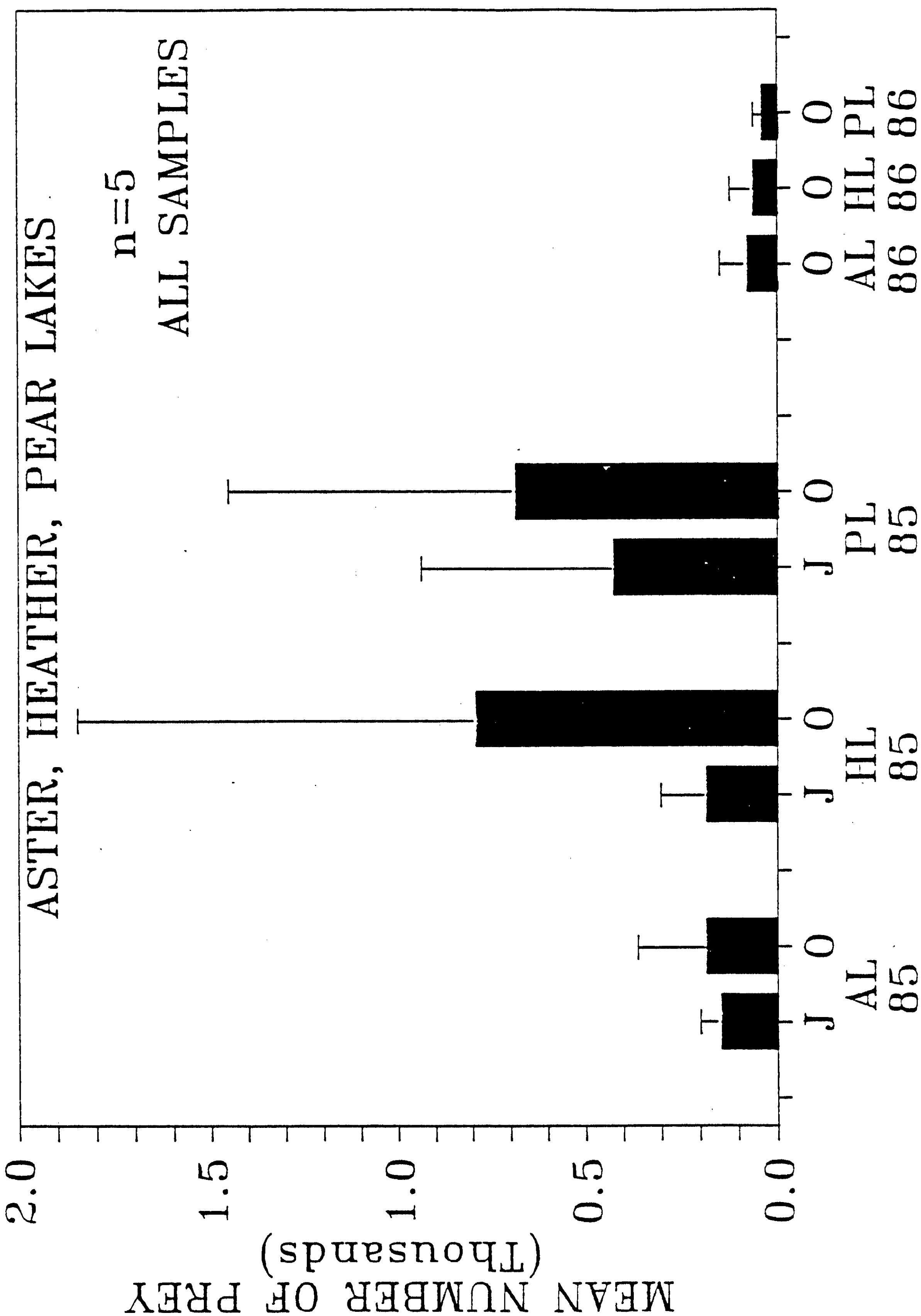


Fig. IX-36. Percent, by number, of various invertebrate groups in the diet of adult Emerald Lake brook trout, July-November, 1985-1987.

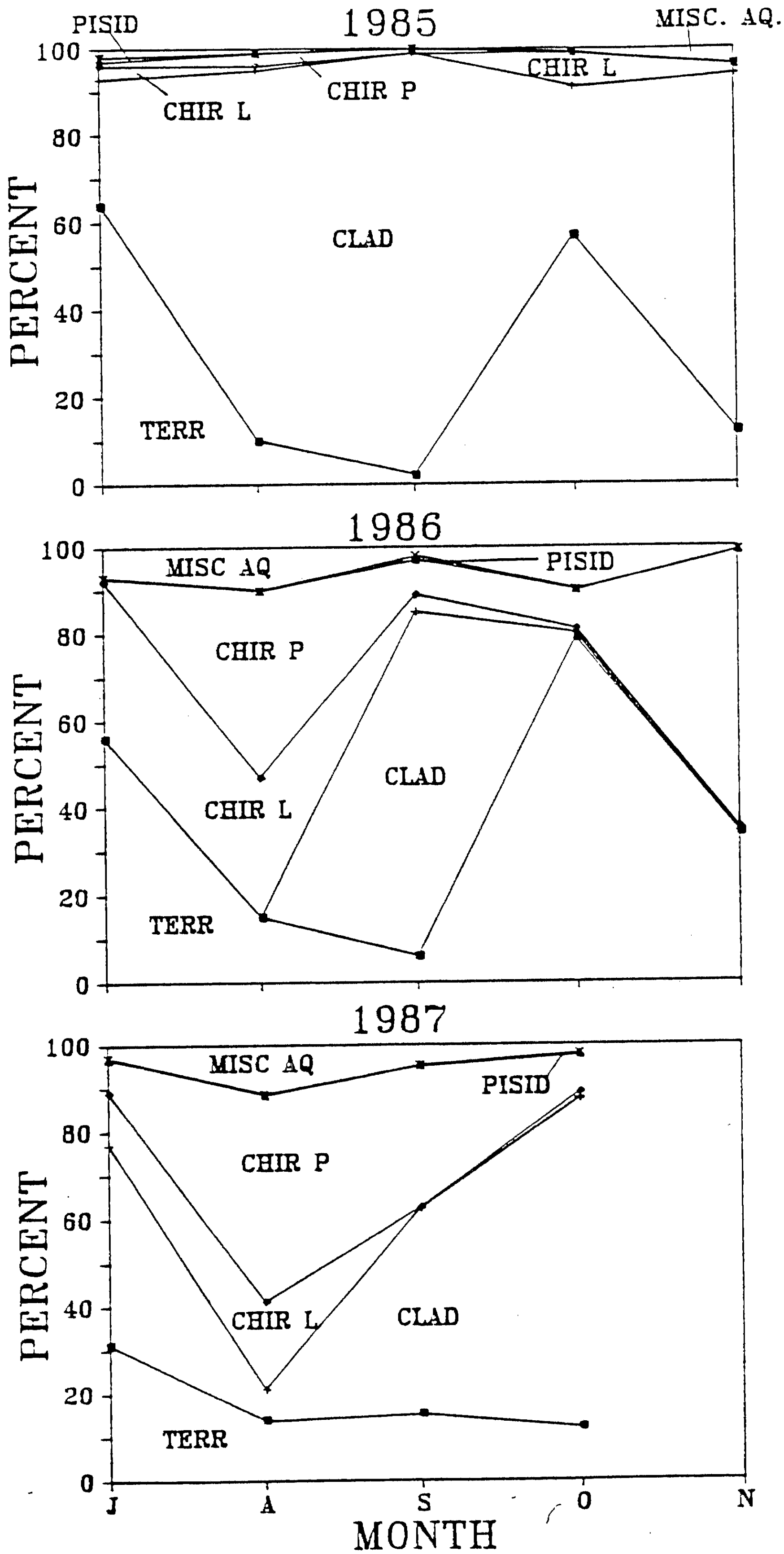


Fig. IX-37. Percentage of adult brook trout stomachs from Emerald Lake containing the 4 major taxonomic groups, 1985-1987.

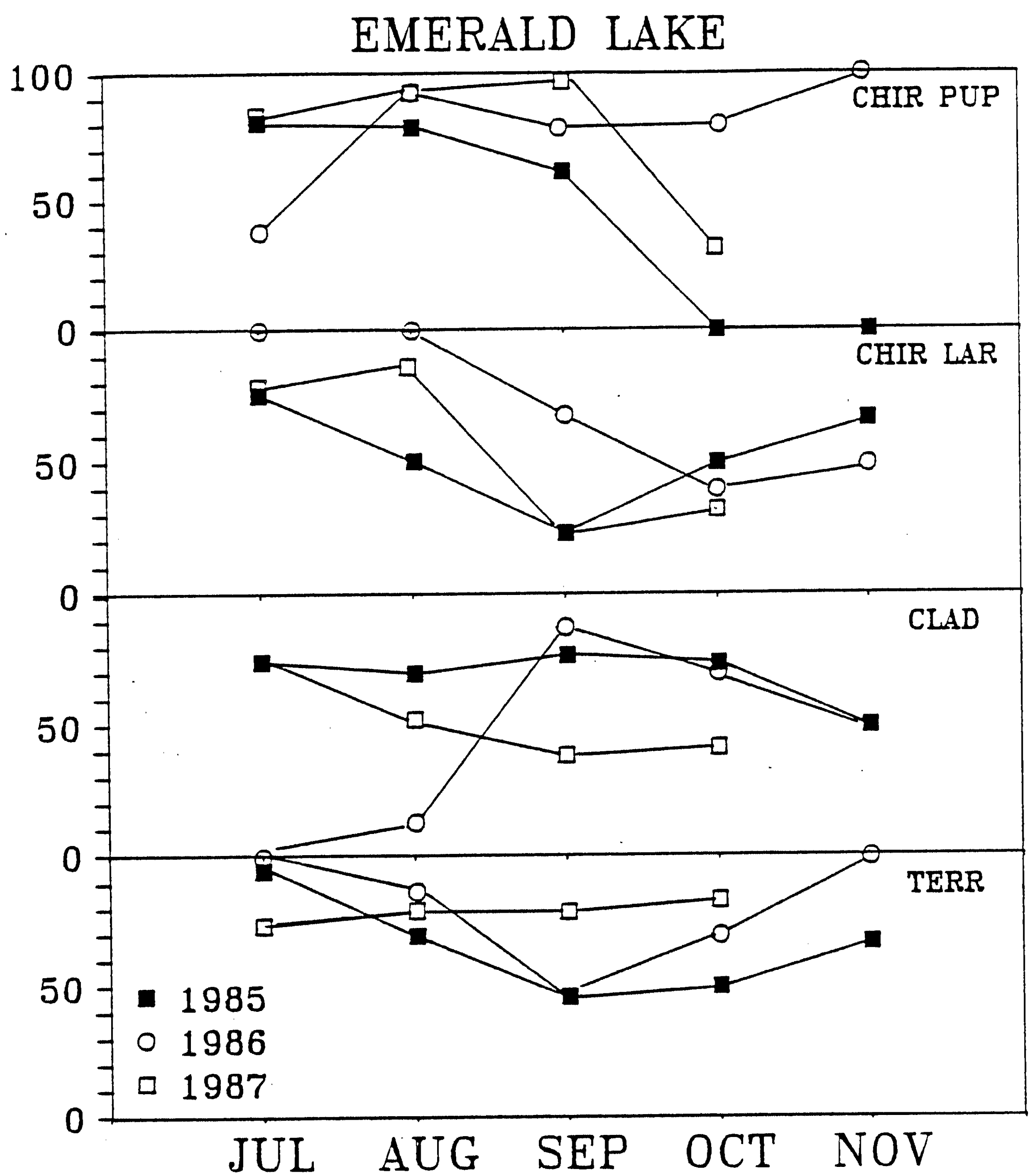


Fig. IX-38. Percentage of adult brook trout stomachs from Emerald Lake containing Daphnia rosea and Eurycercus lamellatus during the summers of 1985-1987.

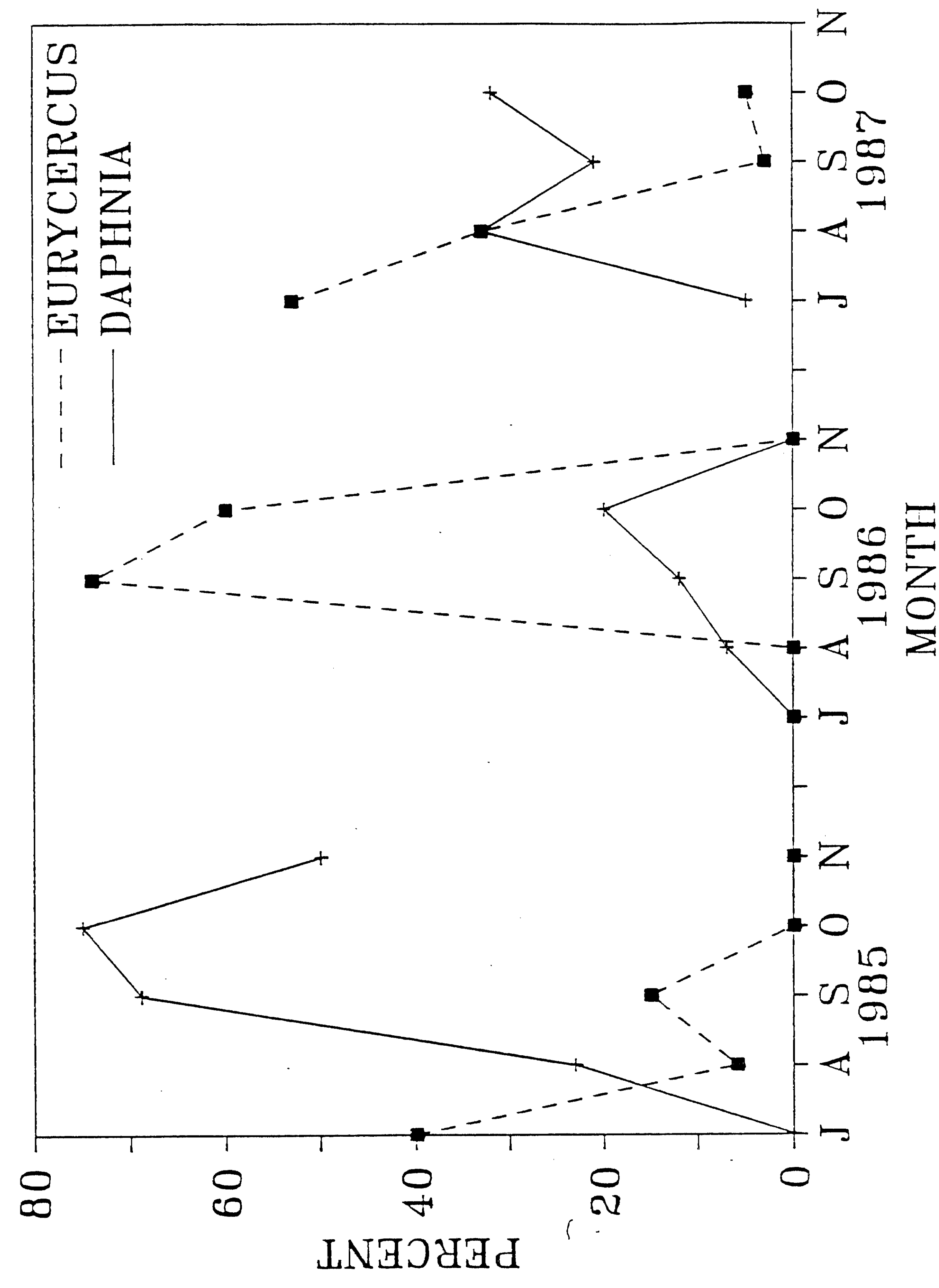


Fig. IX-39. Percent, by number, of various invertebrate groups in the diet of adult brook trout from Aster, Heather and Pear lakes, July and October 1985.

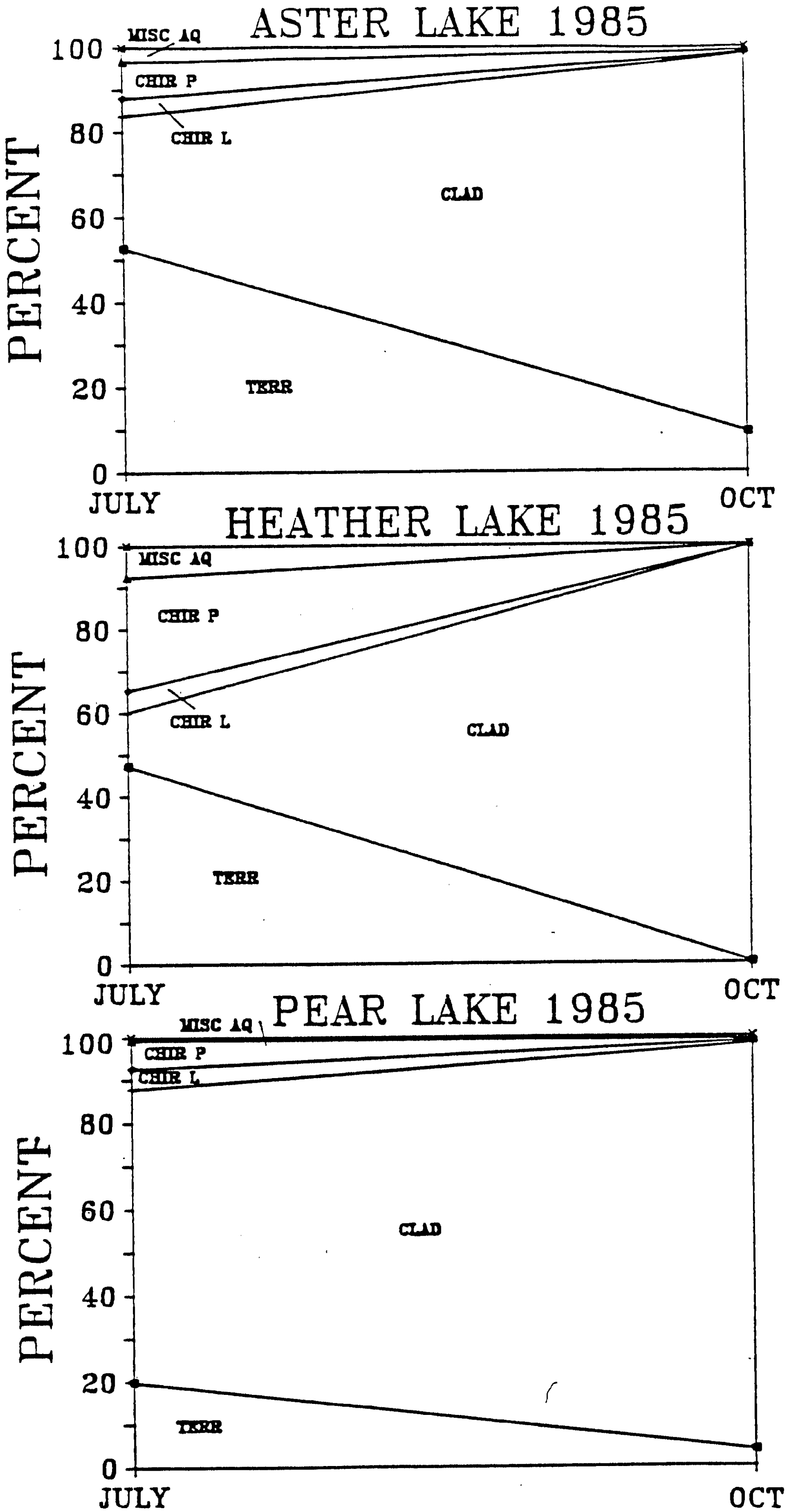


Fig. IX-40. Percent of adult fish containing various prey groups in Aster, Heather and Pear lakes, July and October 1985.

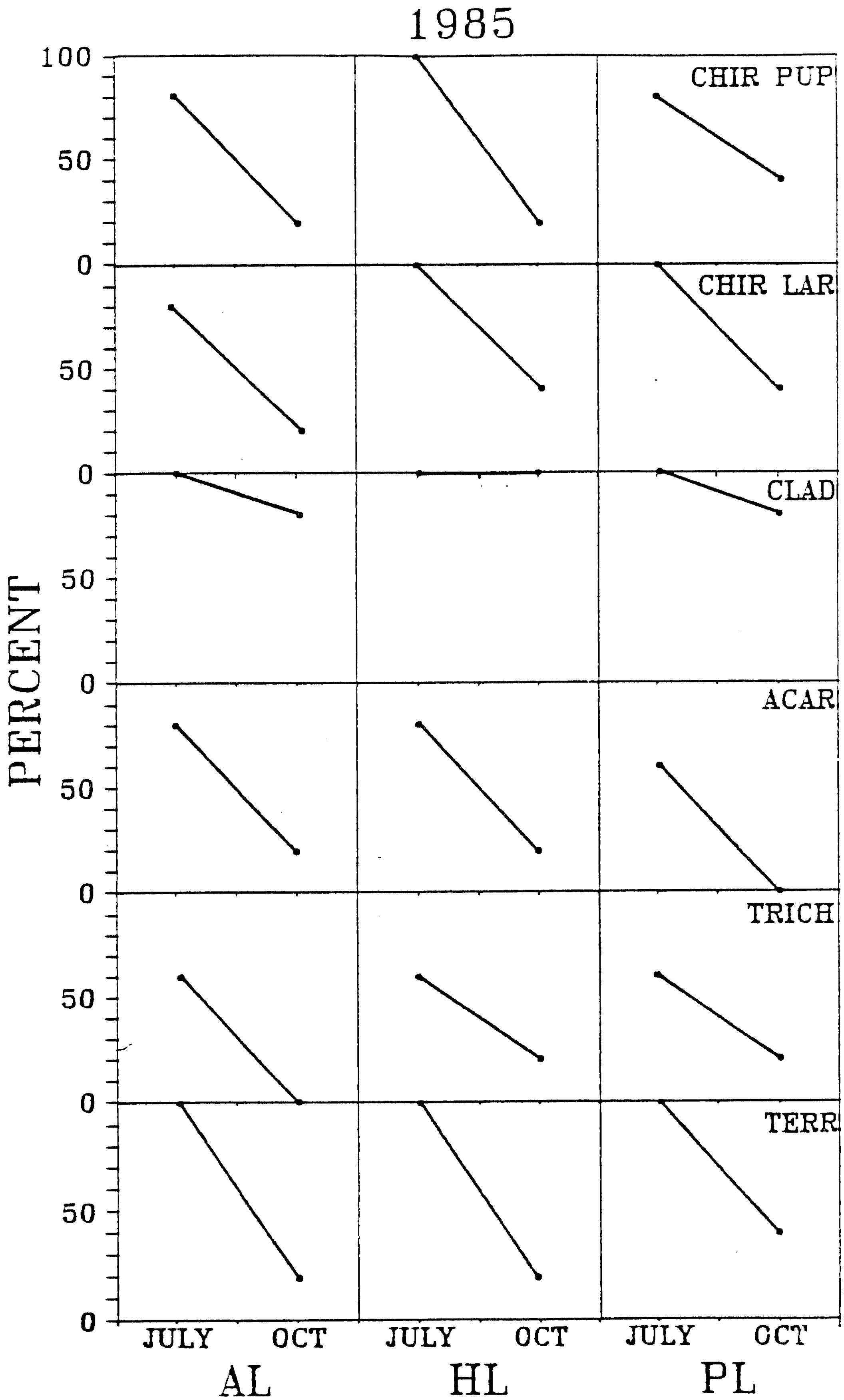


Fig. IX-41. Percent of adult fish containing various prey groups in Aster, Heather and Pear lakes, October 1986.

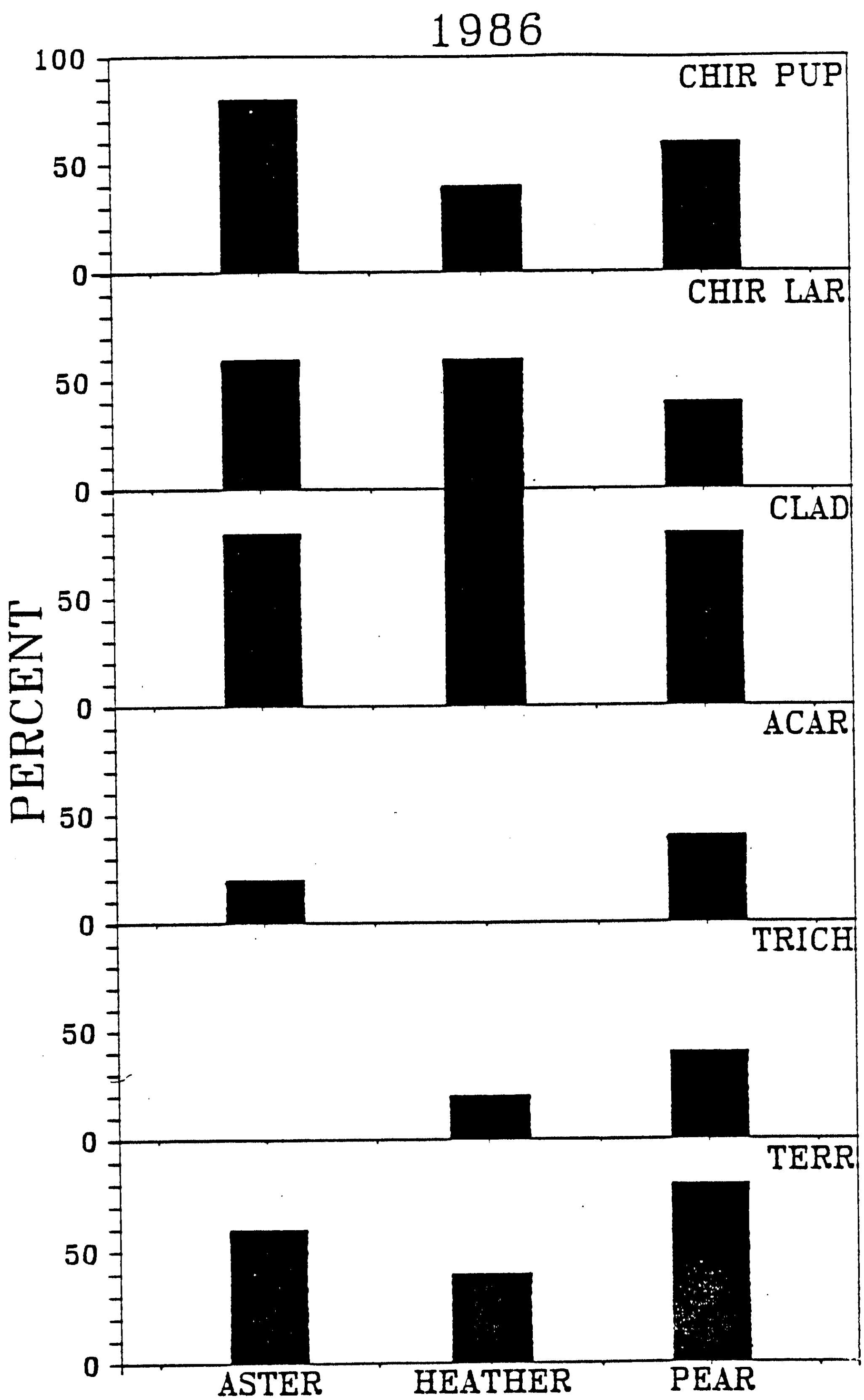


Fig. IX-42. Mean numbers of prey in the stomachs of fish from the Emerald outlet, July 1985-Sep 1986. Bars are 95% confidence limits.

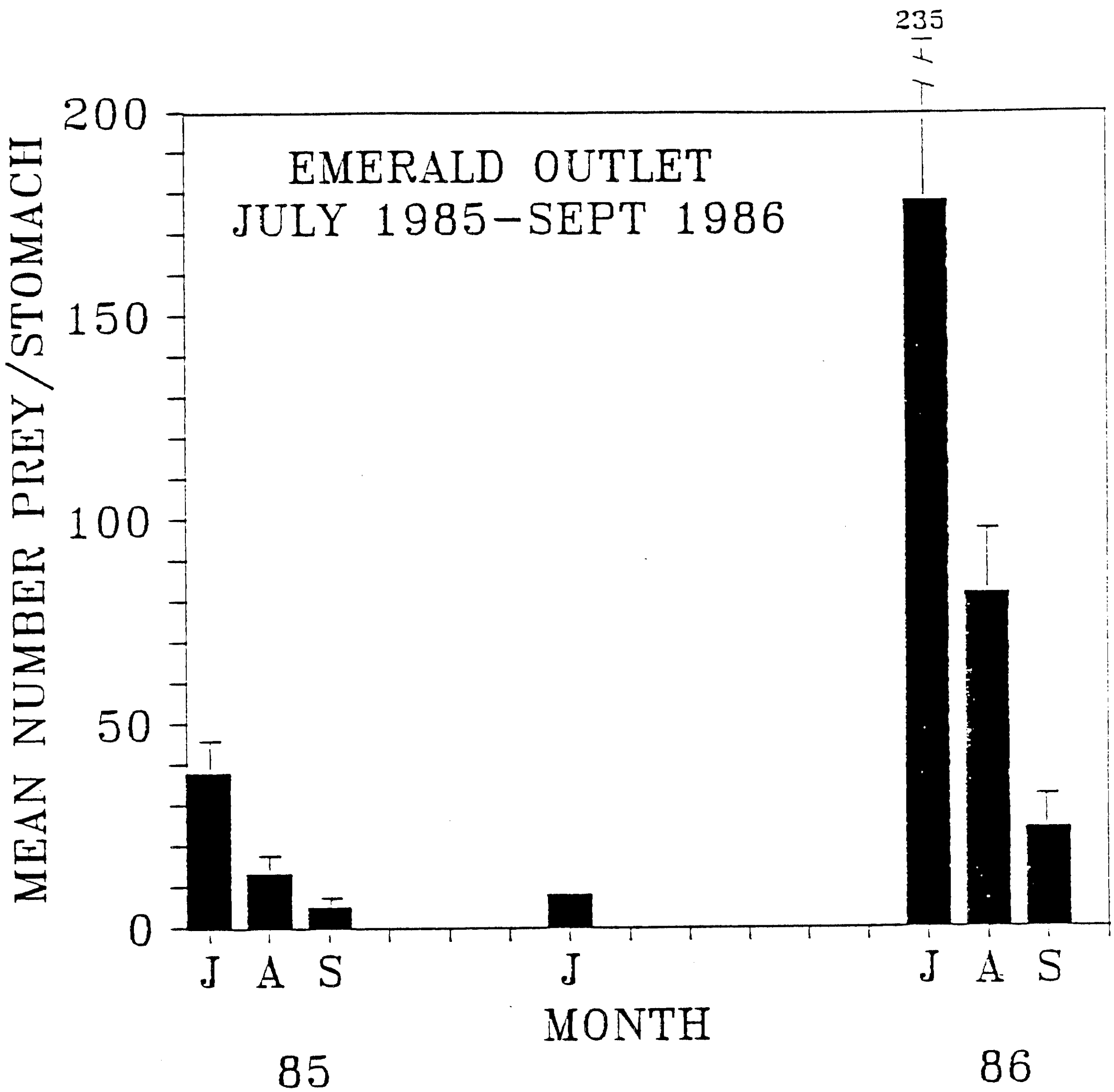


Fig. IX-43. Mean numbers of prey in the stomachs of 0+ brook trout in Emerald outlet, 1985-1987. Vertical lines are 95% confidence intervals. Numbers above bars are sample sizes.

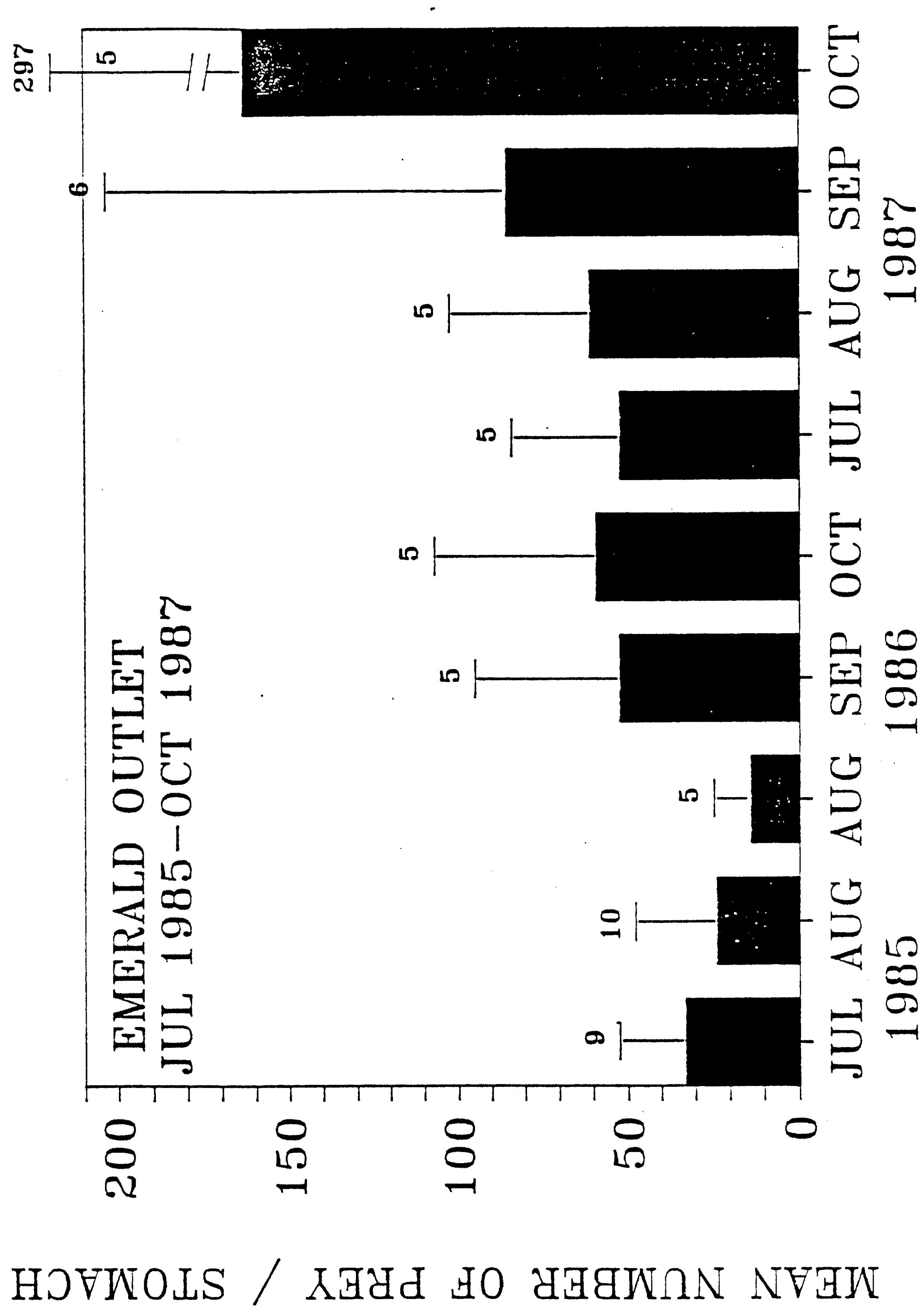


Fig. IX-44. Percent, by number, of various invertebrate groups in the diet of brook trout from the Emerald outlet, July-November, 1985 and 1986.

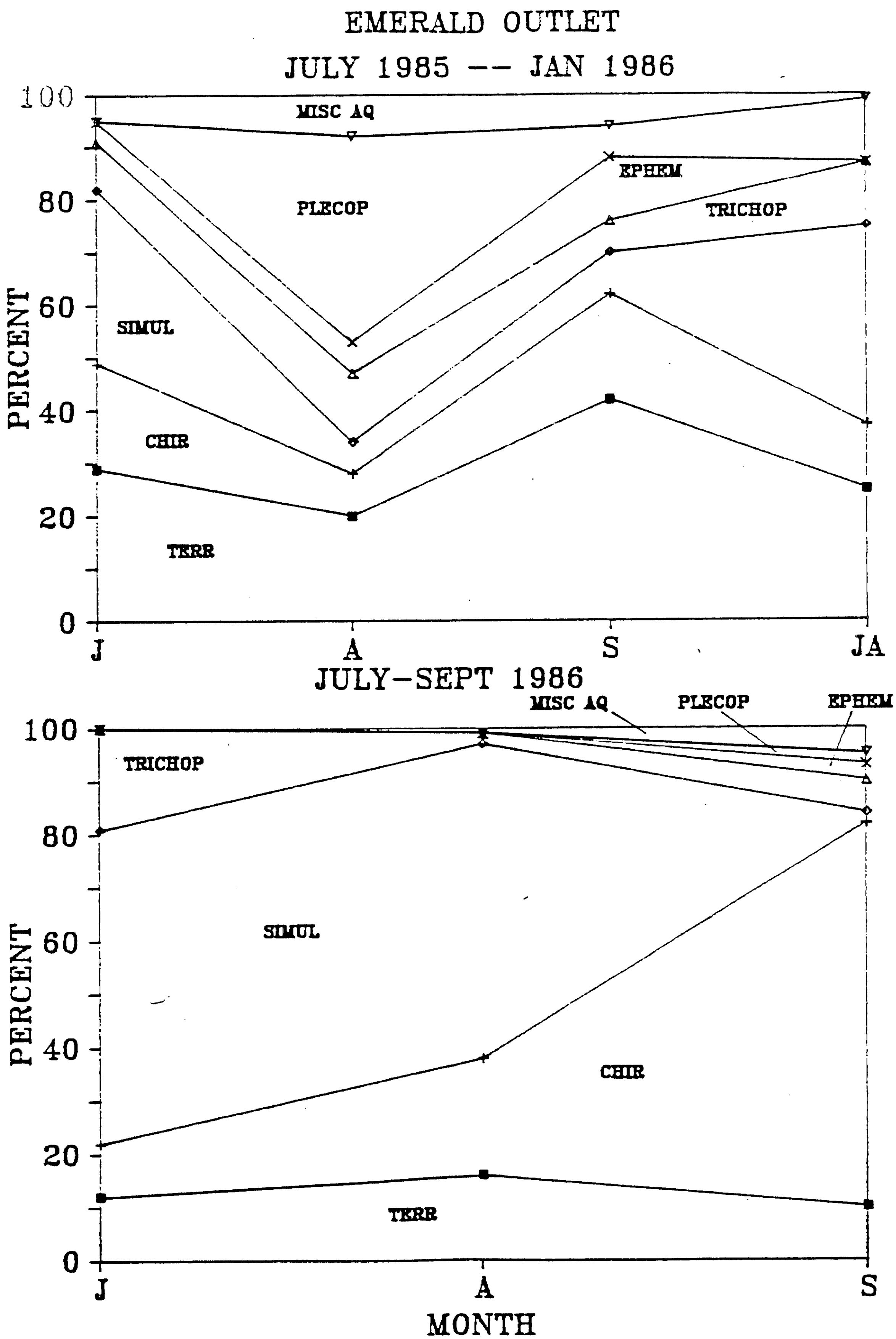


Fig. IX-45. Percentages of juvenile and adult brook trout from the Emerald outlet whose stomachs contained the 6 major prey taxa, 1985 and 1986.

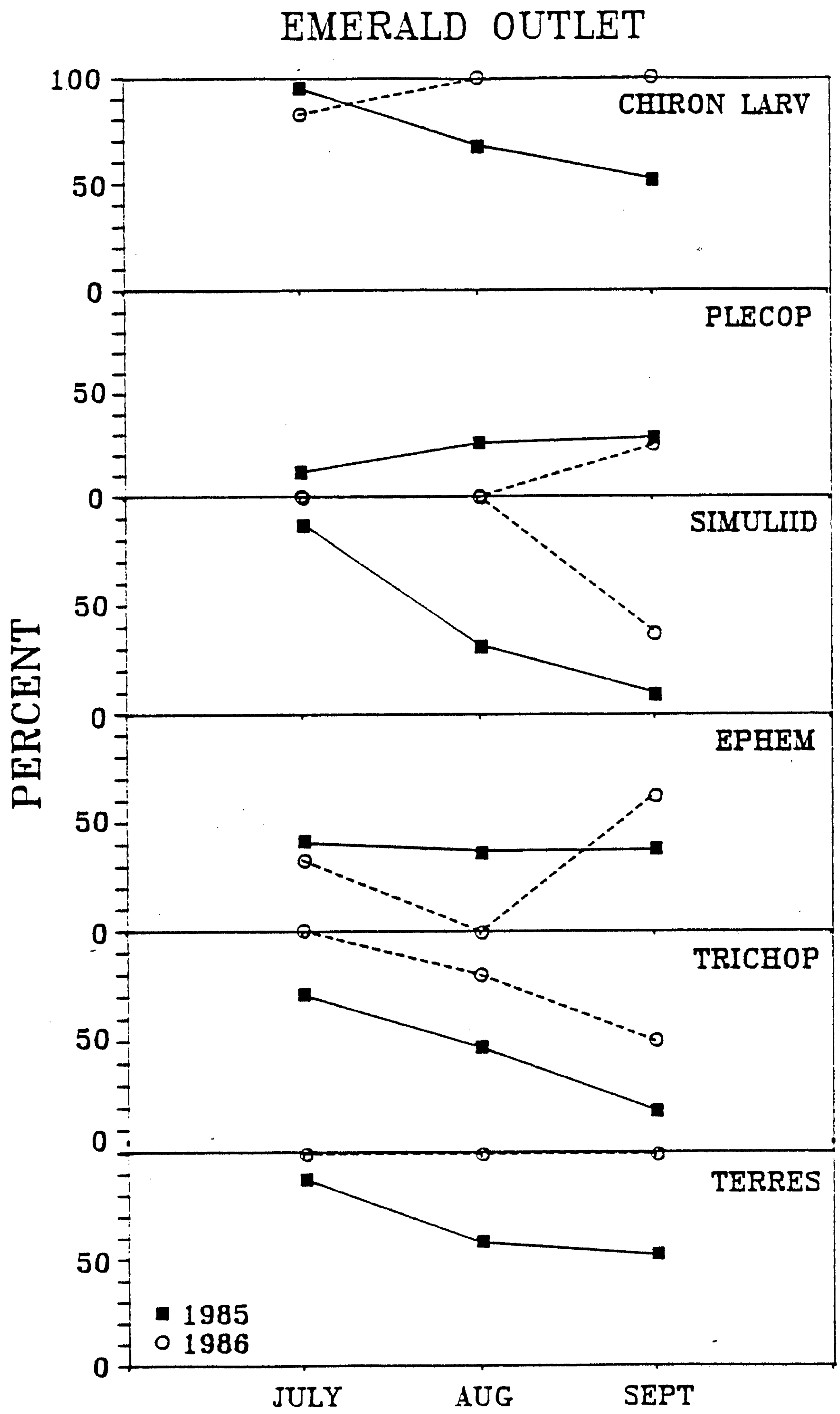


Fig. IX-46. Mean numbers of prey in the stomachs of 0+ brook trout in Pond 1, 1986 and 1987. Vertical lines are 95% confidence intervals. Numbers above bars are sample sizes.

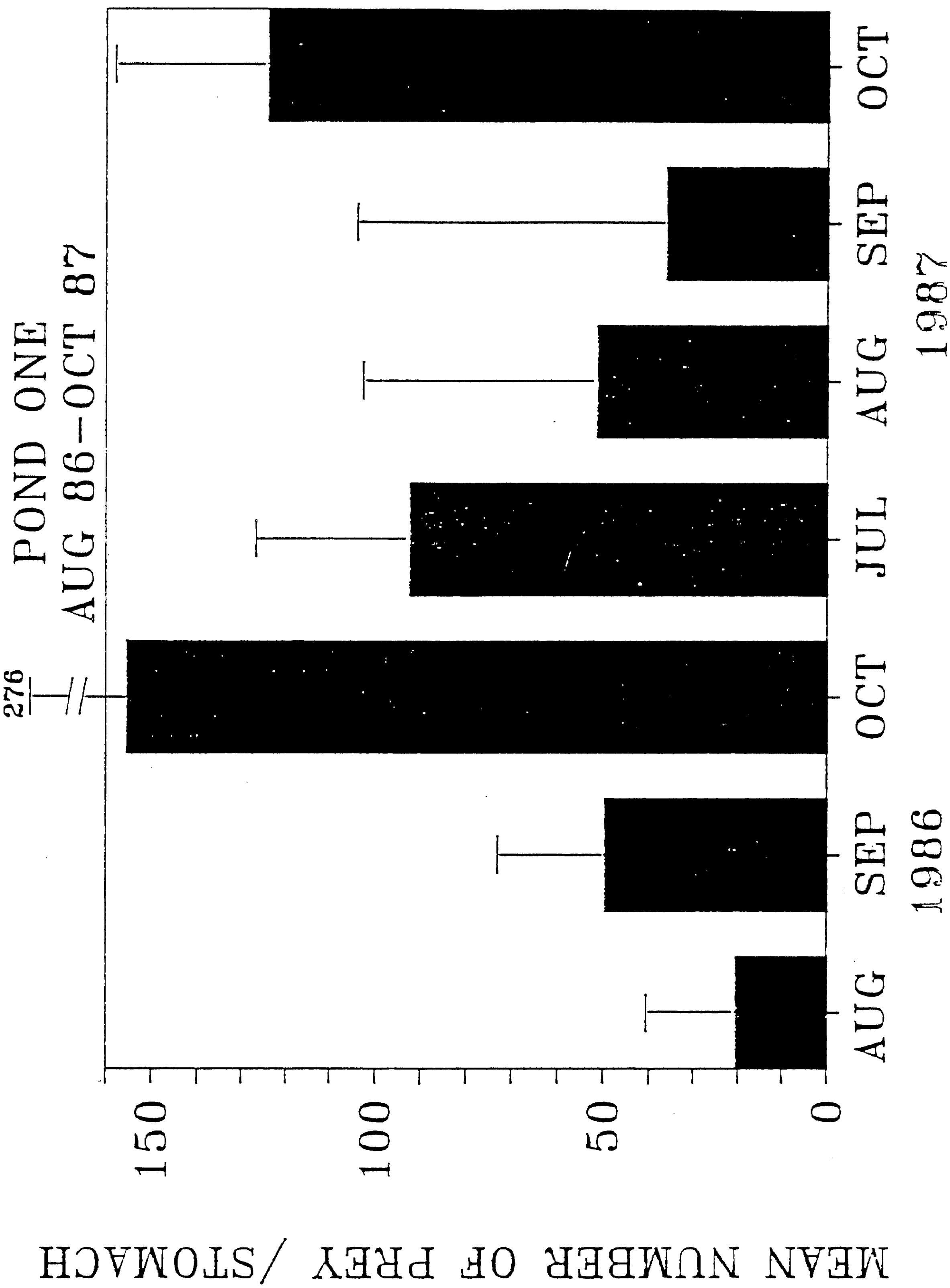


Fig. IX-47. Average distance to the water surface and to the bottom for 0+ brook trout observed in the Emerald Lake basin during the summer of 1987.

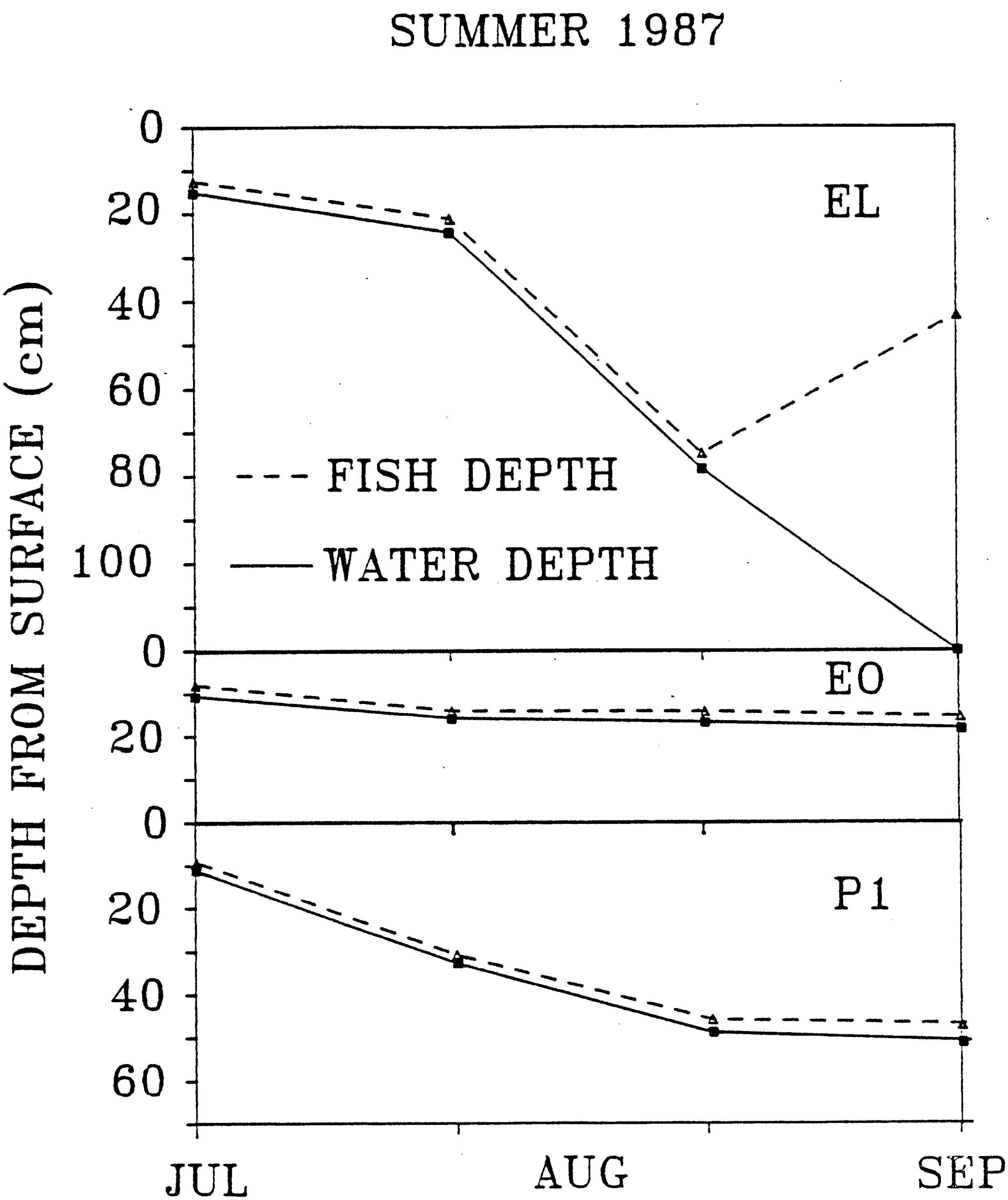
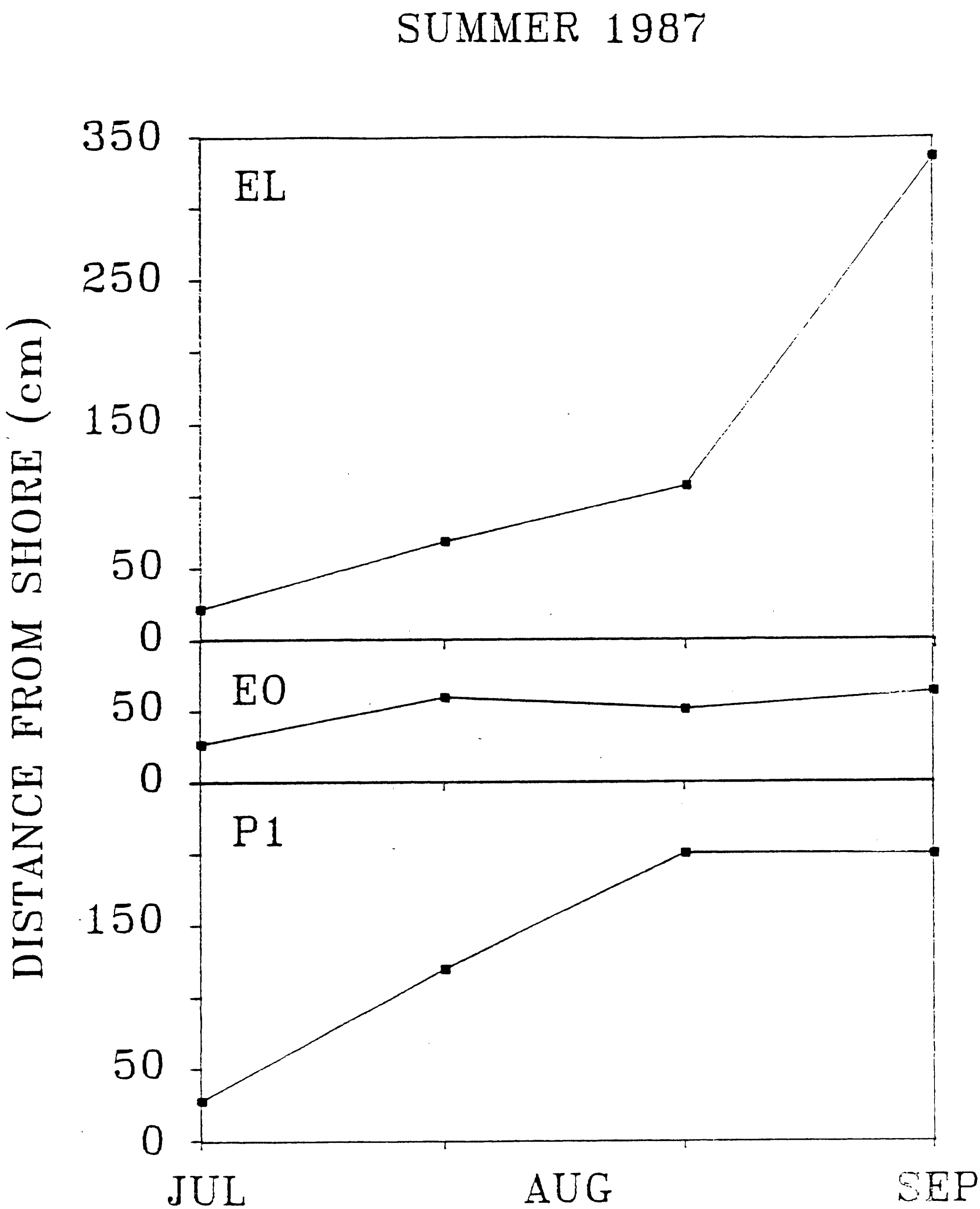


Fig. IX-48. Distance from shoreline for 0+ brook trout observed in the Emerald Lake basin during the summer of 1987.



Chapter X

Survey of Lakes in the Kaweah River (Marble Fork) Basin

Acid deposition is known to have profound impacts on the composition of zooplankton, benthic invertebrate, and fish communities (Almer et al. 1974, NRC Canada 1981, Kimmel et al. 1986, Hall and Ide 1987). Effects on aquatic organisms can often be related to direct effects of H^{+} ions or to increased mobilization and concentration of trace (Gran 1980, Hall et al. 1987), interfering with metabolic and ion-exchange processes (le Croix et al. 1985) and reproductive physiology (McDonald 1983). Alteration of community assemblages may also be the result of indirect acid effects modifying trophic level interactions as sensitive prey species are reduced, eliminated and/or replaced by more tolerant taxa (e.g. Burton et al. 1982, Burton and Allan 1986).

Detection of the loss of species and alteration of community composition may prove an important early-warning system for determining the impacts of acid deposition. In order to detect community changes potentially attributable to acidification, an intensive monitoring program is necessary to define natural spatial and temporal variation in species distributions and abundances. Because intensive sampling is necessary to characterize even one system, most monitoring efforts focus on one system. It is important, however, to know if the study system is representative of other systems in a given area, before the results can be extrapolated to larger areas.

In this chapter, we report the results of a chemical and biological survey of lakes in the basin of the Kaweah River (Marble Fork), and we compare these lakes with our intensive study site, Emerald Lake. The purpose of this survey is to determine if Emerald Lake is representative of lakes throughout the Kaweah River drainage.

Methods

Chemical and biological characteristics of 8 lakes and a vernal pond in the Kaweah River drainage were monitored on an annual basis beginning in 1984. The lakes and their approximate elevations are as follows: Aster- 2700 m, Emerald- 2800 m, Heather- 2800 m, Pear- 2900 m, Hidden- 3000 m, Topaz- 3200 m, Frog- 3000 m, Lyness- 3100 m, and a vernal pond- 3100 m (see Figure I-1 for locations). The first 5 lakes have large reproducing populations of brook trout (Salvelinus fontinalis); the last 4 are fishless. The lakes were sampled in August and September from 1984-87. Profiles of temperature and dissolved oxygen were measured at the deepest part of each lake, and water samples were collected from near the surface for analysis of specific conductance, pH, acid neutralizing capacity (ANC), major ions, ammonium, phosphate, silica, and, beginning in 1985, for total iron, aluminum, and manganese. Sampling and analytical methods are described in Chapter II.

Zooplankton was sampled by taking duplicate vertical tows with a 12-cm net (63-µm mesh). Single tows were taken from fishless lakes in 1986. Samples were preserved in 12% formalin and identified and counted under a dissecting microscope at 12X. The presence or absence of zooplankton taxa was determined for each lake from 1984 to 1987. Quantitative densities were additionally determined for 1986 and 1987.

Benthic macroinvertebrates were sampled qualitatively with sweep nets (D-nets, 250-µm mesh). Sweep samples were taken along the margins of each lake. Samples were also collected from the outflow streams of each lake using the D-net as a modified "kick net". Sometimes the outflows were dry on sampling dates (Heather-1985, 1986, 1987; Hidden-1986, 1987; Frog, Aster, Lyness, Pear, and Topaz-1987). Sampling intensity (measured as time) was identical in all lakes. Macroinvertebrates were preserved in 70% ethanol until identification at 25X under a dissecting microscope.

Statistical analyses of the relationship between zooplankton and macroinvertebrate species richness and elevation were performed with a Spearman rank correlation on combined data from all sample dates. To correct for differences in the number of annual samples collected among lakes, we determined the frequency of occurrence of each zooplankton and macroinvertebrate taxon in each lake. This measure was a ratio of the years each taxon was collected in samples from a lake to the number of years that the lake was sampled. Analyses contrasting the community structure of fish and fishless lakes over all four years were then performed on individual taxa using the Mann-Whitney *U*-test. Analyses contrasting fish and fishless lake zooplankton community structure were additionally performed on individual taxa with the Mann-Whitney *U*-test for discrete year samples from both 1986 and 1987.

Results

Chemistry

All of the lakes sampled in the survey were generally similar in chemistry to Emerald Lake (Table X-1). Ionic proportions were usually similar; all lakes are calcium-bicarbonate waters, although sodium was sometimes equal in concentration to calcium. Compared with the survey lakes, Emerald Lake had a slightly lower pH, and slightly higher concentrations of nitrate and sulfate. With the exception of Pear Lake, the total ionic contents of the survey lakes were slightly higher than that of Emerald Lake. The peak in chloride in Frog Lake in 1987 is unusual because it was not accompanied by peaks in the other major ions, and may therefore be anamolous. Most of the lakes were more dilute in 1986 than in the other years, as was Emerald Lake. Concentrations of phosphate and ammonium, which are not included in Table X-1, were close to our analytical detection limits in all of the lakes.

Zooplankton

Twenty-three species of zooplankton were collected, including two calanoid copepods, two cyclopoid copepods, 10 cladocerans, and nine rotifers (Table X-2). The number of species collected from lakes ranged from 4 (Lyness Lake) to 13 (Heather Lake) in individual years and from 9 (Hidden) to 17 (Aster and Heather) over all four years (Table X-2). Depending on the year, from 7 to 10 species were collected from Emerald Lake, including one copepod, five cladocerans, and four rotifers. The number of species collected in lakes tended to decline with increasing elevation across all lakes (Spearman's $r_s = -0.72$, $p < 0.05$). Most of the increase in species richness with declining elevation resulted from increases in the species richness of cladocerans and rotifers. There were also differences in the species composition of zooplankton assemblages in lakes with and without trout. The large calanoid copepod _Diaptomus eiseni_ and the large cladoceran _Daphnia middendorfianna_ (when present) were collected in all fishless lakes but were absent in all lakes containing fish (Mann-Whitney *U*-test, P's = 0.02) (Table X-2). On the other hand, _Daphnia rosea_ and _Chydorus sphaericus_ were present more frequently in lakes with trout but were absent or reduced in abundance in lakes lacking trout (Mann-Whitney *U*-test P's $\leq$ 0.04) (Table X-2). _D. rosea_ was significantly more abundant in lakes containing trout in both 1986 and 1987 (p's = 0.02) than in those without trout (Tables X-3, X-4, and X-5). Small species such as

Keratella serrulata and Trichocerca capucina were collected more frequently from lakes with brook trout (Mann-Whitney *U*-test P's ≤ 0.02), and reached high abundances only in trout lakes (Table X-2). Both K. taurocephala and T. capucina were more dense in trout lakes during 1986 and 1987 (P's ≤ 0.05) compared to those without trout (Tables X-3, X-4, X-5). Although Diaptomus signicauda was an important member of the zooplankton assemblage in all lakes (Table X-2), it reached higher densities in lakes without trout than those with trout in 1986 (P = 0.03) (Tables X-3 and X-5). Holopedium gibberum was found in significantly higher densities in lakes with trout in 1986 (Mann-Whitney *U*-test, P = 0.03) (Tables X-3 and X-5).

The zooplankton assemblage of Emerald Lake was very similar to that found in Pear Lake, a lake of similar elevation containing trout. Despite elevational gradients, the dominant species found in Emerald Lake (Diaptomus signicauda, Daphnia rosea, Bosmina longirostris, Keratella cochlearis, Polyarthra vulgaris) were dominant or common in other lakes containing brook trout.

Zoobenthos

A total of 32 macroinvertebrate taxa were identified from the lakes in the Kaweah River drainage (Table X-6). The Chironomidae, the water mites (Hydracarina), and the alderfly (Sialis) were present in all lakes and in the vernal pond. Groups found in all permanent water bodies but excluded from the vernal pond were the fingernail clam (Pisidium sp.), oligochaetes, leeches (Hirudinea), and a dytiscid beetle (Deronectes).

The number of macroinvertebrate taxa collected in sweep samples from the lakes ranged from 10 (Heather Lake) to 18 (Frog Lake) with a mean of 11 (s.d.= 5). Species richness tended to decline with increasing elevation both across all lakes and in those containing trout (r_s = 0.72 and 0.89, respectively; P ≤ 0.05). Most of the decline in species richness with increasing elevation resulted from declines in odonate and coleopteran species. A total of 13 taxa were collected from Emerald Lake, including all of the most common taxa (those found in over 50% of the other lakes). Emerald Lake shared 86% of its taxa with two other lakes, and 57% with 5 of the remaining lakes. The community composition at Emerald Lake was most similar to those lakes which also had brook trout, containing 86% of the taxa found in those communities. In comparison, only 50% of the taxa found in fishless lakes were also found in Emerald Lake (this difference, however, was not significant: p = 0.23, Fisher's

Exact Test). There was a significant absence of Callibaetis, hemipterans, and a dytiscid beetle (Hydroporus) from trout lakes (Mann-Whitney *U*-test, P's $\leq$ 0.03). Conversely, the frequency of occurrence of the odonate Zoniagrion was significantly tied to the presence of trout (Mann-Whitney *U*-test, P = 0.01).

Outflow streams

A greater number of taxa (44) was collected in the outflow streams than in the lakes. Taxa richness ranged from 6 (Hidden Lake) to 22 (Frog Lake) with a mean of 16 (s.d.= 5). Emerald outflow samples contained 19 taxa (Table X-7). The Chironomidae, Oligochaeta, Simuliidae, and Hydracarina were present in all stream communities. Slightly less widespread were baetid mayfly nymphs (Baetis), nemourid stonefly larvae (Zapada), and predatory caddisfly larvae (Rhyacophila); these taxa were present in 6, 6, and 5 outflows, respectively, in at least one year. Species richness of outflow streams was positively related to the permanence of the habitat (r_s = 0.77 P = 0.05), ranging from 15-22 taxa in streams that remained flowing or dried only one year of the study, compared to 2-6 taxa in those that dried in 2 or 3 of the study years (Table X-7).

The Emerald Lake outflow contained all of the common species found throughout the Kaweah basin. Of the 8 taxa found in over 4 of the stream communities, 7 were found in the Emerald outflow. The only taxon not found was the adult stage of the dytiscid beetle Deronectes sp.

The macroinvertebrate assemblages of outflow streams were also related to trout presence. Hemipterans (Sigara and Notonecta), the muscid Limnophora, and dytiscid beetles (Agabus and Deronectes) were absent or occurred less frequently in lakes with fish than in fishless lakes (Mann-Whitney *U*-test, P's $\leq$ 0.04).

Discussion

Elevation and presence of trout are the most important determinants of zooplankton community composition in lakes in the Marble Fork catchment. These results agree with those of Stoddard (1986), who sampled 75 lakes in the Sierra Nevada including Emerald, Pear, and Heather Lakes. Stoddard (1986) reported species complements in Emerald, Pear, and Heather Lakes that are similar to the ones that we found. In conjunction with our results, the species composition of Sierran lakes appears to remain relatively constant over time. In accordance with our results, a number of investigators have observed decreasing zooplankton species richness with increasing elevation (Stoddard 1986, Patalas 1964, Reed and Olive 1958). In addition, the presence of trout had an effect on the distribution of zooplankton species; large species (maximum size > 2 mm) were found only in fishless lakes, and some small species (maximum size < 1.2 mm) were present or dominant only in lakes with trout. It has long been known that large zooplankton will be eliminated by trout predation to the benefit of some small species (Brooks and Dodson 1965).

The zooplankton assemblage in Emerald Lake is typical of those found in high elevation lakes containing brook trout (Stoddard 1986). In addition, the species found in Emerald Lake are widely distributed in the western U.S. and Canada (Stoddard 1986, Neill 1984 and 1985). In general, then, the results of our zooplankton investigations in Emerald Lake should have wide implications for lake systems in western North America.

The most apparent pattern in the distribution of macroinvertebrates in the Kaweah drainage was related to the presence of brook trout (Salvelinus fontinalis). The capacity of fish to profoundly influence invertebrate assemblages has been well documented in zooplankton prey assemblages (Zaret 1980). Similar studies of lake macroinvertebrate communities are rare, but suggest that lakes containing few or no fish generally contain conspicuous taxa which are largely absent from lakes with greater numbers of fish (Bendell and McNicol 1987). Prey vulnerability to fish predation is generally related to prey size, activity and exposure (Healy 1981, Hemphill and Cooper 1984, Cooper 1988). Species absent from trout communities in this study are generally large and/or mobile, conspicuous taxa, including baetids (Callibaetis), hemipterans (Sigara and Notonecta), and dytiscid beetles (Agabus and Deronectes). The observed distributions of these species were not related to elevation.

There are a large number of macroinvertebrate species in Emerald Lake with broad distribution in the Kaweah drainage. These include the Ephemeroptera, sphaeriid clams, and plecopterans, all known to be intolerant of acid conditions (Roff and Kwiatkowski 1977, Friberg et al. 1980, Singer 1982, Mackay and Kersey 1985, Cooper et al. 1988, Hopkins et al. 1988). The most common taxa are also present in lakes in Kings Canyon National Park, located north of the Kaweah basin (Taylor and Erman 1980).

We conclude that the chemical and biological characteristics of Emerald Lake and its outflow are similar to those of other lakes in the Kaweah basin. Differences in the zooplankton and macroinvertebrate assemblages among lakes can be explained largely by elevation and the presence or absence of fish. However, most Sierran lakes contain fish, as does Emerald Lake. Conclusions based on our detailed investigations of Emerald Lake should therefore apply generally to lakes throughout the Kaweah River drainage, and are relevant to high-elevation lakes throughout the Sierra Nevada.

Table X-1. Selected chemical variables for lakes in the basin of the Kaweah River (Marble Fork). Data on Emerald Lake are included for comparison. Emerald Lake data are means for August-September samples from 1.0-m depth. The other lakes were sampled once each year, in August or September, at the surface. Concentration units are $\mu eq\ L^{-1}$.

Lake	Year	pH	ANC	Ca^{2+}	Na^{+}	Mg^{2+}	K^{+}	SO_4^{2-}	NO_3^{-}	Cl^{-}
Aster	1984	6.4	35	25	11	5.5	3.5	5.5	0.2	3.6
	1985	6.6	45	24	25	5.6	4.4	7.1	0.3	4.6
	1986	6.4	35	--	--	--	--	4.9	0.0	1.9
	1987	6.4	31	29	19	5.0	4.5	6.6	0.3	4.7
	mean	**6.4**	**37**	**26**	**18**	**5.4**	**4.1**	**6.0**	**0.2**	**3.7**
Topaz	1984	6.6	43	34	11	5.2	3.7	6.3	0.0	3.1
	1985	6.6	31	24	17	4.5	2.2	5.8	2.7	6.3
	1986	6.4	27	8.7	7.3	2.2	1.1	3.2	0.0	1.4
	1987	6.2	--	30	15	4.0	2.9	5.5	0.0	3.1
	mean	**6.5**	**34**	**24**	**13**	**4.0**	**2.5**	**5.2**	**0.7**	**3.5**
Frog	1984	6.8	69	54	16	4.6	5.4	5.4	1.3	5.5
	1985	6.8	61	45	15	4.1	3.2	4.9	1.2	3.6
	1986	6.6	42	--	--	--	--	3.6	0.4	2.8
	1987	6.6	56	21	27	3.6	4.1	7.3	0.2	24
	mean	**6.7**	**57**	**40**	**19**	**4.1**	**4.2**	**5.3**	**0.8**	**9.0**
Heather	1984	6.4	46	33	12	7.4	8.2	3.7	0.1	11
	1985	6.5	46	29	21	6.4	3.5	4.4	2.0	5.9
	1986	6.4	47	--	--	--	--	3.8	0.0	3.1
	1987	--	--	--	--	--	--	--	--	--
	mean	**6.4**	**46**	**31**	**17**	**6.9**	**5.9**	**4.0**	**1.1**	**6.7**
Hidden	1984	--	--	--	--	--	--	--	--	--
	1985	6.6	44	32	11	3.7	2.5	2.8	0.2	1.8
	1986	--	--	--	--	--	--	--	--	--
	1987	6.5	42	38	36	4.1	4.7	5.9	0.0	6.1
	mean	**6.5**	**43**	**35**	**23**	**3.9**	**3.6**	**4.3**	**0.1**	**3.9**
Pear	1984	6.4	22	17	7.0	3.4	2.2	3.8	0.1	2.4
	1985	6.4	25	17	15	4.0	3.2	4.8	2.5	2.9
	1986	6.3	27	--	--	--	--	4.8	0.0	2.5
	1987	6.4	27	53	39	4.7	20	4.4	0.0	6.1
	mean	**6.4**	**25**	**29**	**20**	**4.0**	**8.5**	**4.5**	**1.3**	**3.5**
Emerald	1984	6.3	23	20	11	5.1	3.4	6.0	2.5	2.6
	1985	6.3	30	22	12	3.9	2.8	5.9	2.1	2.2
	1986	6.4	33	20	9.3	2.5	2.2	5.1	1.1	3.5
	1987	6.3	27	22	11	4.3	3.4	7.2	3.7	2.6
	mean	**6.3**	**28**	**21**	**11**	**3.9**	**2.9**	**6.1**	**2.4**	**2.7**

Table X-2. Frequency (# ocurrences / # years sampled) of zooplankton taxa collected from lakes in the Kaweah (or Tokapah) drainage in August, September, and October 1984 - 1987.

	Lake	Years sampled	Diaptomus signicauda	Diaptomus eiseni	Macorcyclops albidus	Tropocyclops prasinus	Daphnia rosea	Daphnia middendorfiana	Diaphanosoma brachyurum	Ceriodaphnia affinis	Holopedium gibberum	Bosmina longirostris	Polyphemus pediculus	Macrothrix montana	Chydorus sphaericus	Alona affinis	Keratella taurocephala	Keratella serrulata	Polyarthra vulgaris	Conochilus unicornis	Trichocerca capucina	Ploesoma sp.	Lepadella sp.	Ascomorpha sp.	Salvelinus fontinalis	Number of species
FISHLESS LAKES	Topaz	4	1.0	1.0	.25	0	0	.25	0	0	0	.25	0	0	.25	0	.75	0	.75	.75	.75	0	0	0	--	10
	Frog	4	1.0	1.0	0	0	.25	.50	0	0	.25	.75	0	.25	.25	0	1.0	0	1.0	0	0	0	0	0	--	10
	Lyness	3	1.0	1.0	.33	0	.33	.33	0	0	0	0	0	0	0	.33	.66	0	.66	1.0	.33	0	0	0	--	10
FISH LAKES	Hidden	2	1.0	0	.50	0	1.0	0	0	0	0	0	0	0	.50	0	1.0	1.0	1.0	.50	1.0	0	0	0	+	9
	Pear	4	0	0	.25	0	1.0	0	.25	0	0	1.0	.25	0	.50	0	1.0	.25	1.0	.75	1.0	.50	0	.25	+	14
	Emerald	4	1.0	0	0	0	1.0	0	0	0	.75	1.0	.50	0	.25	0	1.0	.25	1.0	.75	1.0	0	0	0	+	10
	Aster	4	1.0	0	.5	0	1.0	0	.75	1.0	.50	1.0	.50	0	.50	.50	1.0	.25	1.0	.50	1.0	.50	0	.25	+	17
	Heather	4	1.0	0	.75	.25	1.0	0	.50	1.0	.75	1.0	0	0	.75	.50	1.0	.25	1.0	0	1.0	.50	.25	.25	+	17

Table X-3. Zooplankton taxa, mean densities (M^{-3}) $\pm$ 1 S.E., and number of species collected from lakes in the Kaweah (or Tokapah) drainage in August, September, and October 1986.

	Lake	Date	*Diaptomus signicauda*	*Diaptomus eiseni*	*Macorcyclops albidus*	*Daphnia rosea*	*Ceriodaphnia affinis*	*Holopedium gibberum*	*Bosmina longirostris*	*Polyphemus pediculus*	*Chydorus sphaericus*	*Alona affinis*	*Keratella taurocephala*	*Keratella serrulata*	*Polyarthra vulgaris*	*Conochilus unicornis*	*Trichocerca capucina*	*Salvelinus fontinalis*	Number of species
FISHLESS LAKES	Topaz	26 Aug 86																	
		mean	101679	50	0	0	0	0	0	0	0	0	505	0	33623	3876	164	--	6
		s.e.	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		
	Frog	26 Aug 86																	
		mean	18551	883	0	0	0	0	71	0	0	0	2544	0	7032	0	0	--	5
		s.e.	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		
	Lyness	26 Aug 86																	
		mean	12308	5236	127	0	0	0	0	0	0	60	69	0	69	216	0	--	7
		s.e.	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		
FISH LAKES	Pear	10 Sep 86																	
		mean	768	0	0	381	0	646	39	0	0	0	11580	0	7536	1845	519	+	8
		s.e.	27	--	--	--	--	105	6	--	--	--	221	--	2144	77	11		
	Emerald	8 Oct 86																	
		mean	5325	0	0	37	0	1471	372	0	0	0	44697	93	48226	0	242	+	8
		s.e.	931	--	--	37	--	168	149	--	--	--	8086	93	5116	--	19		
	Aster	10 Sep 86																	
		mean	6843	0	0	1313	1944	1187	3232	294	147	0	199109	0	4413	13	303	+	11
		s.e.	1893	--	--	353	76	177	252	294	147	--	14867	--	2064	13	101		
	Heather	10 Sep 86																	
		mean	3741	0	30	1266	177	825	824	0	0	0	80250	0	71576	0	589	+	9
		s.e.	559	--	29	206	59	354	117	--	--	--	6465	--	16318	--	59		

Table X-4. Zooplankton taxa, mean densities (M^{-3}) ± 1 S.E., and number of species collected from lakes in the Kaweah (or Tokapah) drainage in August, September, and October 1987.

	Lake	Date	Diaptomus signicauda	Diaptomus eiseni	Macorcyclops albidus	Daphnia rosea	Ceriodaphnia affinis	Diaphonasoma brachyurum	Holopedium gibberum	Bosmina longirostris	Polyphemus pediculus	Chydorus sphaericus	Alona affinis	Keratella taurocephala	Keratella serrulata	Polyarthra vulgaris	Conochilus unicornis	Trichocerca capucina	Lecane sp.	Salvelinus fontinalis	Number of species
FISHLESS LAKES	Topaz	16 Sep 87																			
		mean	6427	884	0	0	0	0	0	0	0	0	0	38	0	13	0	0	0	--	4
		s.e.	1856	50	--	--	--	--	--	--	--	--	--	13	--	13	--	--	--		
	Frog	17 Sep 87																			
		mean	20310	177	0	88	0	0	133	44	0	0	0	1770	0	167810	0	0	0	--	7
		s.e.	4026	88	--	0	--	--	133	0	--	--	--	442	--	21637	--	--	--		
	Lyness	17 Sep 87																			
		mean	39624	132	0	0	0	0	0	0	0	0	0	310	0	1681	6228	266	0	--	6
		s.e.	5797	132	--	--	--	--	--	--	--	--	--	133	--	266	2224	266	--		
FISH LAKES	Hidden	17 Sep 87																			
		mean	3143	0	19	98	0	0	0	0	0	39	0	202996	29219	20309	59	1356	0	+	10
		s.e.	550	--	19	20	--	--	--	--	--	39	--	103389	2353	10093	39	491	--		
	Pear	17 Sep 87																			
		mean	74	0	0	1988	0	0	0	110	0	7	0	11841	324	14610	412	280	0	+	9
		s.e.	15	--	--	132	--	--	--	96	-	7	--	589	206	1767	118	59	--		
	Emerald	1 Oct 87																			
		mean	41769	0	0	37	0	0	0	364	0	0	0	51613	0	5260	2107	1457	0	+	7
		s.e.	2810	--	--	37	--	--	--	364	-	--	--	1717	0	578	838	936	--		
	Aster	9 Sep 87																			
		mean	4022	0	88	3226	2011	561	177	1083	0	0	884	105541	94	60552	6	110	0	+	13
		s.e.	309	--	88	1282	376	561	0	552	--	--	884	29818	94	7216	6	66	--		
	Heather	1 Sep 87																			
		mean	5530	0	198	11487	29	0	464	3336	0	405	0	879705	0	383969	0	913	59	+	11
		s.e.	2172	--	81	2533	29	--	287	729	-	125	--	174889	--	57857	--	88	59		

Table X-5. Significant differences in abundances of zooplankton taxa collected from fish and fishless lakes in the Kaweah (or Tokapah) drainage in August, September, and October of 1986 and 1987. U = Mann - Whitney statistic.

	Year			
	1986		1987	
Taxa	Fish lakes (n = 4)	Fishless lakes (n = 3)	Fish lakes (n = 5)	Fishless lakes (n = 3)
Diaptomus signicauda		p =.03 u = 12		
Diaptomus eiseni		p =.02 u = 12		p =.01 u = 15
Daphnia rosea	p =.02 u = 0		p =.02 u = 0	
Holopedium gibberum	p =.02 u = 0			
Keratella taurocephala	p =.03 u = 0		p =.02 u = 0	
Trichocerca capucina	p =.02 u = 0		p =.05 u = 1	

Table X-6. Frequency of occurrence (# years collected / # years sampled) of macroinvertebrate taxa collected using qualitative sweep nets and Ekman grabs from Tokapah Drainage lakes, Aug. - Sept. 1984-87. (Number of years collected).

	Fish lakes					Fishless lakes		
Taxa	(4) Aster	(4) Emerald	(2) Heather	(4) Pear	(3) Hidden	(4) Topaz	(4) Frog	(4) Lyness
O. Ephemeroptera								
F. Baetidae								
g. Callibaetis	.50	0	0	.50	.66	.75	.75	.75
O. Odonata								
F. Aeshnidae								
g. Aeshna	.25	0	0	.50	0	0	0	0
F. Libellulidae								
g. Sympetrum	0	.50	0	.50	0	0	0	0
Coenegrionidae								
g. Zoniagrion	.50	.75	1.0	.50	0	0	0	0
O. Hemiptera								
F. Corixidae								
g. Sigara	.25	0	0	0	0	1.0	1.0	.50
F. Gerridae								
g. Gerris	0	.50	0	.50	0	1.0	1.0	1.0
F. Notonectidae								
g. Notonecta	.25	0	0	0	.33	.75	.50	1.0
O. Megaloptera								
F. Sialidae								
g. Sialis	.50	.75	1.0	.75	.66	.25	.75	.75
O. Trichoptera								
F. Lepidostomidae								
g. Lepidostoma	.50	0	0	0	0	0	0	0
F. Limnephilidae								
g. Dicosmoecus	0	0	0	.50	0	0	0	.75
g. Ecclisomyia	0	.50	.50	.75	0	0	.25	0
g. Hesperophylax	0	0	0	0	0	.50	1.0	0
g. Onocosmoecus	0	0	0	0	0	0	0	.25
F. Psychomiidae								
g. Tinodes	0	.50	0	0	0	.25	0	0
F. Rhyacophilidae								
g. Rhyacophila	.50	.25	0	0	0	0	.25	0
O. Coleoptera								
F. Dytiscidae								
g. Acilius	0	0	0	0	0	0	0	0
g. Agabus	0	0	0	0	0	.25	0	0
g. Deronectes	.75	.50	0	.50	.66	.75	.75	.50
g. Hydroporus	0	0	0	0	0	.25	.25	.50
g. Hydrovatus	0	0	0	0	.33	0	0	0
g. Hygrotus	0	0	0	0	0	.25	.25	0
g. Oreodytes	0	0	1.0	0	0	0	.50	0

Table X-6 (continued). Frequency of occurrence (# years collected / # years sampled) of macroinvertebrate taxa collected using qualitative sweep nets and Ekman grabs from Tokapah Drainage lakes, Aug. - Sept. 1984-87. (Number of years collected).

	Fish lakes					Fishless lakes		
	(4)	(4)	(2)	(4)	(3)	(4)	(4)	(4)
Taxa	Aster	Emerald	Heather	Pear	Hidden	Topaz	Frog	Lyness
F. Elmidae								
g. *Narpus*	.75	0	0	0	0	0	0	0
F. Hydrophilidae								
g. *Tropisternus*	.50	0	0	0	0	0	0	0
O. Diptera								
F. Chironomidae	1.0	1.0	1.0	1.0	.66	.75	1.0	1.0
F. Ceratopogonidae								
g. *Bezzia*	0	.50	0	0	0	0	0	0
F. Simulidae								
g. *Simulium*	.75	0	0	.25	0	.25	.25	0
Empididae								
g. *Clinocera*	.75	0	0	0	0	0	0	0
O. Hydracarina	.50	.75	1.0	.75	.33	.75	.50	.25
O. Heterodonta								
F. Sphaeridae								
g. *Pisidium*	1.0	1.0	1.0	.75	.66	.75	1.0	.75
O. Oligochaeta	0	.25	1.0	.75	.66	.75	.75	
F. Hirudinea	.75	.50	.25	.50	.33	.50	.25	.50
Total Number of Taxa	18	13	10	14	10	17	18	14

Table X-7. Frequency of occurrence (# years collected / # years sampled) of macroinvertebrate taxa collected using qualitative sweep nets from Tokapah Drainage lake outlets, Aug. - Sept. 1984-87. (Number of years collected).

	Fish lakes					Fishless lakes		
Taxa	(3) Aster	(4) Emerald	(1) Heather	(3) Pear	(2) Hidden	(3) Topaz	(3) Frog	(3) Lyness
O. Trichoptera								
F. Limnephilidae								
g. Dicosmoecus	0	.25	0	.66	0	0	0	0
g. Ecclisomyia	0	.75	0	1.0	0	0	.66	.33
g. Hesperophylax	0	0	0	0	0	.33	.66	0
g. Onocosmoecus	0	0	0	0	0	0	0	.33
F. Psychomyiidae								
g. Tinodes	0	.50	0	0	0	0	.33	0
F. Rhyacophilidae								
g. Rhyacophila	1.0	.50	0	1.0	1.0	0	1.0	.33
O. Coleoptera								
F. Dytiscidae								
g. Agabus	0	0	0	0	.50	.33	1.0	.66
g. Deronectes	.33	0	0	0	0	.66	.66	.33
g. Hydroporus	0	0	0	0	0	.33	0	0
g. Hydrovatus	0	0	0	0	0	.33	0	0
g. Oreodytes	0	0	0	.33	0	0	.66	0
F. Elmidae								
g. Narpus	1.0	0	0	.33	0	0	0	0
g. Rhizelmus	1.0	0	0	0	0	0	0	0
F. Hydrophilidae								
g. Helophorus	0	0	0	0	0	0	.66	0
g. Tropisternus	1.0	0	0	0	0	0	0	0
O. Diptera								
F. Chironomidae	1.0	.50	0	1.0	1.0	.66	1.0	.66
F. Tipulidae								
g. Dicranota	0	.50	0	0	0	.33	.33	.33
F. Empididae								
g. Clinocera	1.0	0	0	0	0	0	0	0
F. Muscidae								
g. Limnophora	0	0	0	0	0	.33	.33	.33
F. Simulidae								
g. Prosimulium	0	.50	0	.33	0	0	0	0
g. Simulium	1.0	.50	0	1.0	.50	.33	1.0	.33
O. Hydrocarina	.66	.50	1.0	.33	1.0	.66	1.0	.33
O. Heterodonta								
F. Sphaeridae								
g. Pisidium	1.0	0	0	.33	0	.33	.33	0
O. Oligochaeta	.66	.75	1.0	.66	1.0	1.0	1.0	.66
Total Number of Taxa	22	20	2	15	9	15	22	15
No. of years dried up	1	0	3	1	2	1	1	1

Table X-7 (continued). Frequency of occurrence (# years collected / # years sampled) of macroinvertebrate taxa collected using qualitative sweep nets from Tokapah Drainage lake outlets, Aug. - Sept. 1984-87. (Number of years collected).

	Fish lakes					Fishless lakes		
	(3)	(4)	(1)	(3)	(2)	(3)	(3)	(3)
Taxa	Aster	Emerald	Heather	Pear	Hidden	Topaz	Frog	Lyness
O. Trichoptera								
F. Limnephilidae								
g. *Dicosmoecus*	0	.25	0	.66	0	0	0	0
g. *Ecclisomyia*	0	.75	0	1.0	0	0	.66	.33
g. *Hesperophylax*	0	0	0	0	0	.33	.66	0
g. *Onocosmoecus*	0	0	0	0	0	0	0	.33
F. Psychomyiidae								
g. *Tinodes*	0	.50	0	0	0	0	.33	0
F. Rhyacophilidae								
g. *Rhyacophila*	1.0	.50	0	1.0	1.0	0	1.0	.33
O. Coleoptera								
F. Dytiscidae								
g. *Agabus*	0	0	0	0	.50	.33	1.0	.66
g. *Deronectes*	.33	0	0	0	0	.66	.66	.33
g. *Hydroporus*	0	0	0	0	0	.33	0	0
g. *Hydrovatus*	0	0	0	0	0	.33	0	0
g. *Oreodytes*	0	0	0	.33	0	0	.66	0
F. Elmidae								
g. *Narpus*	1.0	0	0	.33	0	0	0	0
g. *Rhizelmus*	1.0	0	0	0	0	0	0	0
F. Hydrophilidae								
g. *Helophorus*	0	0	0	0	0	0	.66	0
g. *Tropisternus*	1.0	0	0	0	0	0	0	0
O. Diptera								
F. Chironomidae	1.0	.50	0	1.0	1.0	.66	1.0	.66
F. Tipulidae								
g. *Dicranota*	0	.50	0	0	0	.33	.33	.33
F. Empididae								
g. *Clinocera*	1.0	0	0	0	0	0	0	0
F. Muscidae								
g. *Limnophora*	0	0	0	0	0	.33	.33	.33
F. Simulidae								
g. *Prosimulium*	0	.50	0	.33	0	0	0	0
g. *Simulium*	1.0	.50	0	1.0	.50	.33	1.0	.33
O. Hydrocarina	.66	.50	1.0	.33	1.0	.66	1.0	.33
O. Heterodonta								
F. Sphaeridae								
g. *Pisidium*	1.0	0	0	.33	0	.33	.33	0
O. Oligochaeta	.66	.75	1.0	.66	1.0	1.0	1.0	.66
Total Number of Taxa	22	20	2	15	9	15	22	15
No. of years dried up	1	0	3	1	2	1	1	1

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